ECOLOGICAL MONOGRAPHS

VOL. I OCTOBER, 1931 NO. 4

OFFICIAL PUBLICATION OF THE
ECOLOGICAL SOCIETY OF AMERICA

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PUBLISHED QUARTERLY BY
THE DUKE UNIVERSITY PRESS
DURHAM, N. C., U.S.A.

ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL
FOR ALL PHASES OF BIOLOGY

Issued on the fifteenth of December, March, June, and September

The editorial board of this journal will consider ecological papers which are long enough to make twenty-five printed pages or more. Shorter ecological papers should be submitted to the editor of *Ecology*, which is also published by the Ecological Society of America. Both journals are open to ecological papers from all fields of biological science.

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Entered as Second-class Matter at the Postoffice at Durham, North Carolina.

ECOLOGICAL MONOGRAPHS

VOL. I | OCTOBER, 1931 | NO. 4

THE PLANKTON ECOLOGY OF THE UPPER MISSISSIPPI, MINNEAPOLIS TO WINONA

BY

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THE PLANKTON ECOLOGY OF THE UPPER MISSISSIPPI, MINNEAPOLIS TO WINONA

Introduction

A survey of the Mississippi River was undertaken early in 1928 by the Minnesota Department of Health in coöperation with other agencies in order to ascertain the extent, character, and effect of pollution, and to determine what measures should be taken to remedy the situation. The program for the investigation, besides including a study of the river from a sanitary engineering viewpoint, was designed to bring together corroborative information from bacteriological, chemical, bio-chemical, and biological investigations conducted at the same time. As associate biologist on the stream pollution personnel, I was entrusted with the task of making the plankton examinations according to the scheme suggested by Mr. W. C. Purdy, Special Expert of the United States Public Health Service, Office of Stream Pollution Investigations.

At the termination of the survey it became apparent that a great amount of data had been collected which had no direct bearing upon the stream pollution problem but which could be employed to elucidate certain biological questions connected with the microscopic life of the river. Accordingly I continued the plankton work as a problem of personal research and attempted to analyse my results in the light of the information which had already been gained by the survey and of other information which could be secured by inquiries of my own. This explanation is necessary in order to account for the methods and sources of information which would have been differently balanced if the whole problem had originated as a pure piece of biological research.

The chief purposes of this paper are to present a general picture of the plankton of the upper Mississippi, the relative abundance and seasonal distribution of the constituent organisms, the ecological factors which operate to influence the normal routine of plankton life, and the elucidation as far as possible by qualitative, quantitative, and statistical methods of some of the basic principles which underlie the amazing and complex phenomena exhibited by the plankton of a typical though polluted stream.

The original investigation of the pollution of the Mississippi River covered the section between Minneapolis and La Crosse. The sampling stations were twenty-four in number. From these collections were made at intervals of two weeks. The accompanying map (Fig. 1) shows the location of the sampling points established by the Minnesota Department of Health. It was deemed advisable in the present publication to limit the plankton data to the twelve most significant stations between Minneapolis and Winona, a distance of approximately 130 miles. The original station numbers were retained but those indicated by square frames on the map are not considered in this paper.

A total of over two thousand samples of water were collected from the river and its tributaries and examined during the course of this investigation to obtain the analytical data. The plankton samples numbered 500, but only 250 of these were selected for the purposes of this paper. These samples represent conditions in the river from January to December, 1928.

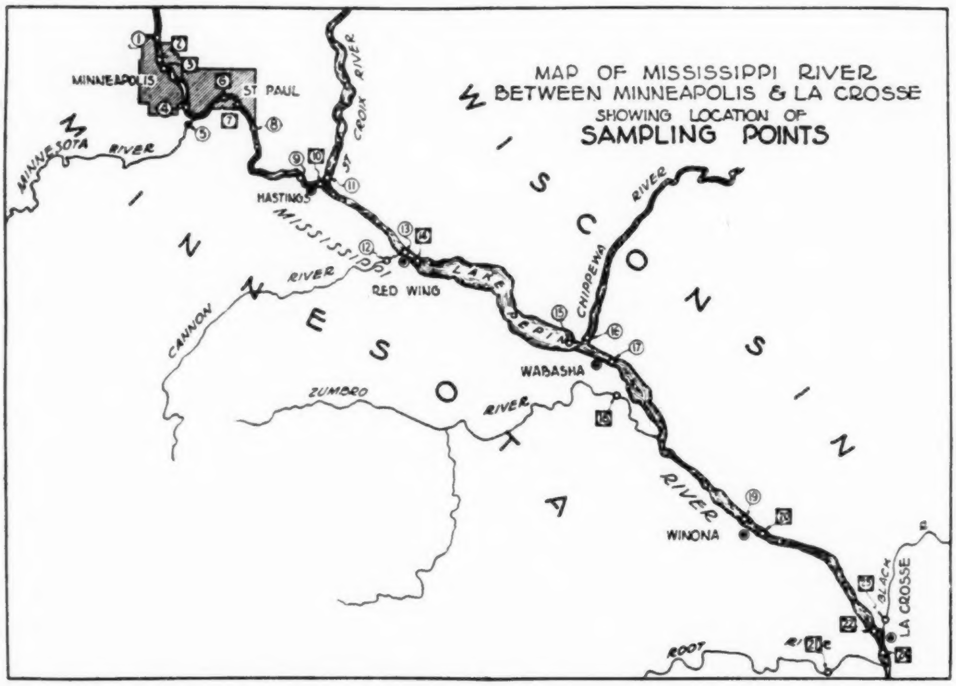


FIG. 1

The Minnesota State Board of Health, Division of Sanitation, supplied the laboratory facilities and equipment, collected the samples, and permitted the use of its extensive records of physical, chemical, and bacteriological analyses. I am greatly indebted to Mr. H. A. Whittaker, director of the division, and to the members of his staff who assisted me in many ways throughout this entire project. An accurate identification of the phytoplankton material would have been impossible without the constant aid of Professor Josephine E. Tilden of the Botany Department of the University of Minnesota, where I carried out most of the microscopic examinations and recorded the basic data. Dr. Royal N. Chapman and Dr. Samuel Eddy were consulted on numerous occasions with regard to the ecological views expressed in this paper, and their advice was most helpful in the compilation and interpretation of the data.

Historical

Preliminary to the extensive coöperative studies of 1928, the pollution of the upper Mississippi River had been the subject of investigation by the

federal government in conjunction with the Health Departments of Wisconsin and of Minnesota. Mr. H. R. Crohurst of the U. S. Public Health Service undertook studies of the river during 1926 and 1927. His report (unpublished) is very rich in matters pertaining to the pollution of the river from the viewpoint of the sanitary engineer, but does not include any biological work. About the same time, Mr. A. H. Wiebe was detailed by the U. S. Bureau of Fisheries to make a biological survey of the same area. His results (1928), relate to the bottom fauna, the plankton, and the fish life of the river. The field work of this survey covered a six weeks period, August 12 to September 27, 1926. The preliminary reports of Crohurst and Wiebe were included in the bulletin entitled "Stream Pollution in Wisconsin" (1927), a report of the Wisconsin Conservation Commission and State Board of Health.

Excluding these specialized pollution investigations and the various hydrographic and water supply papers of the U. S. Geological Survey and other agencies, there is no other publication which deals with the local subject matter of this paper excepting the hydrobiological investigations of P. S. Galtsoff. During the summer of 1921 Galtsoff studied the section of the upper Mississippi between Hastings, Minn. and Alexandria, Mo. in order to determine the composition, amount, and distribution of plankton in various parts of the river and in the lakes with special reference to the fisheries and to the changed conditions created by the Keokuk Dam. His results (1924) are of general limnological interest.

Plankton investigations of the tributaries of the Mississippi River have been limited mainly to four streams, the Illinois, Ohio, Sangamon, and Rock rivers. The plankton of the Illinois River at and near Havana was made the subject of a two-volume memoir by Kofoid (1908), which has become a classic in hydrobiology. Forbes and Richardson (1913, 1919) and Richardson (1921) made further contributions to the biology of this river, and noticed the changes which had occurred as a result of increasing sewage pollution. Purdy also studied pollution conditions in the Illinois River and employed the plankton as "Indicator Organisms." His report has not yet been published.

In 1918 and 1919 a survey of the Sangamon River between Decatur and Springfield, Ill., was made by Minna E. Jewell. The plankton studies were undertaken as a means of gauging conditions of existence and as criteria of the sanitary status of the stream.

The plankton and related organisms of the Ohio River were investigated by Purdy (1921), who made a study of the pollution and natural purification of this large and complicated river system.

The Rock River plankton was recently made the subject of investigation by S. Eddy from the primary aspect of the plankton itself and not in connection with other considerations. This work is still unpublished.

DESCRIPTION OF THE PHYSICAL ENVIRONMENTS

The Mississippi River rises among the numerous glacial lakes in northern Minnesota at an elevation of 1,472 feet above sea level. It flows north, east, and finally south, leaving the state at an elevation of 615 feet. Below Minnesota the river pursues a southerly course of about 1,820 miles to the Gulf of Mexico. Its total length in Minnesota is 658 miles. From its source to the Falls of St. Anthony the river flows almost exclusively through a drift-covered region. For the remainder of its course in Minnesota it occupies an old rocky valley excavated during pre-glacial times. During the first several

TABLE I. *Location of Plankton Sampling Stations on the Mississippi River and Tributaries and Their Respective Drainage Areas*

Station Number	Location	Miles below No. 1	Drainage Areas Sq. Miles
1	Mississippi R. at Camden Bridge, Minneapolis	0	18,850
4	Mississippi R. at Twin City Lock and Dam	10.5	19,000
5	Minnesota R. at mouth, Fort Snelling	12.9	16,500
8	Mississippi R. at Toll Bridge, Inver Grove	28.2	35,700
9	Mississippi R. above Hastings	45.0	36,700
11	St. Croix R. at Toll Bridge, Prescott	47.4	7,290
12	Cannon R. at Bridge on Highway No. 3	66.1	1,440
13	Mississippi R. above Red Wing	68.3	45,800
15	Mississippi R. at outlet of Lake Pepin	95.5	46,500
16	Cheppewa R. at mouth	96.2	9,570
17	Mississippi R. below Wabasha	100.2	56,100
19	Mississippi R. above Winona	131.2	58,600

Comparison of the Physical Characteristics of the Tributaries

	Length of River	Elevation at Source	Elevation at Mouth	Mean Ann. Rainfall in Basin	Slope of Lower River
Minnesota River, Minn.	475	1,896	690	26	0.5 for 112 mi.
St. Croix River, Wis.	170	1,010	672	31	0.3 for 50 mi.
Cannon River, Minn.	100	1,090	665	29	4.9 for 59 mi.
Chippewa River, Wis.	267	1,500	665	30	2.2 for 64 mi.

hundred miles of its journey the river winds between low banks and passes through many lakes and swamps. Below Pokegama Falls the banks become higher, the marshes fewer and a true valley develops.

The Mississippi River enters the Twin City area at Camden, 802 feet above sea level. *Station No. 1* is located in north Minneapolis at the Camden Avenue Bridge. The stream here has a velocity at ordinary stages of about one mile per hour and the bottom is for the most part firm and sandy. The average slope above Camden to Little Falls is 2.6 feet per mile although the slope of the entire Mississippi above the Minnesota River is only 1.4 feet per mile. At this station the river has fairly well recovered from the wastes dis-

charged by municipalities in the upper stretches and has not yet received any sewage from the Twin City area.

Shortly after entering Minneapolis the river passes over the St. Anthony Falls where it drops 70 feet and in so doing leaves the prairie and clay banks for a channel that lies for many miles between rocky bluffs of limestone and sandstone. Two miles above the confluence of the Minnesota, the river again falls a distance of 33 feet at the Twin City Lock and Dam, which was constructed in 1914.

Station No. 4 is located directly above this dam in the pool of relatively quiet water which extends about five miles upstream. The Minneapolis sewage and part of the St. Paul wastes are discharged into the river above this point. As a consequence the bottom of the pool is covered with a thick sludge deposit and foul conditions prevail during the summer especially at times of low water discharge.

At Fort Snelling, a few miles below the Lock and Dam, the Mississippi is joined by the Minnesota, a river which does little to alleviate polluted conditions in the main stream. Fifteen miles further on, at Inver Grove, *Station No. 8* is located. The river has now received the combined sewage and industrial wastes from Minneapolis, St. Paul, South St. Paul, and Newport. Bottom sludges and their organisms indicate a usual state of heavy pollution. The next sampling point on the river is *Station No. 9,* above Hastings and above the confluence of the St. Croix River. The water here is deeper and the current more rapid. Bottom sludges are still heavy but no additional sewage has been added between Inver Grove and this station.

In the interval between Hastings and Red Wing the Mississippi receives the waters of the St. Croix from the east and those of the Cannon from the west. The former is a clean stream with a discharge sufficient to improve appreciably the sanitary quality of the Mississippi; the latter tributary is itself affected by considerable pollution but its discharge is too slight to have any marked effect on the main stream. Below these tributaries and above the town of the Red Wing, *Station No. 13* is located.

From the mouth of the Minnesota River to the State line the Mississippi is a broad, placid stream averaging 1,000 feet across the main channel. About five miles below Red Wing the river fills out its gorge and forms a lake approximately 22 miles in length and about 2 miles in average width. This section of the river is known as Lake Pepin. Here the Mississippi covers its whole flood-plain from bluff to bluff creating a water-covered area of 38.5 square miles with an average depth of 25 to 35 feet in the main portion of the channel. The shore line is comparatively straight with rocky or sandy banks and few sloughs favorable for aquatic vegetation. The bottom consists of mud. Lake Pepin owes its origin to the Chippewa River, which deposited more material into the Mississippi than that great river could carry away. The Chippewa, which has a slope about ten times greater than that of the

Mississippi, was able to form a delta across the main stream which that river, with its slight velocity, could not carry away. At present the entire fall throughout the length of the lake is only 0.5 foot, about 0.02 foot per mile.

The Chippewa River enters from the east. Just above its mouth, in the lake outlet opposite Reads Landing, *Station No. 15* is located. The next station, *No 17,* is below Wabasha, Minn., and represents the river four miles below the confluence of the Chippewa. The last plankton sampling point is at *Station No. 19,* above Winona, 36 miles below the outlet of Lake Pepin. A minor tributary, the Zumbro River, unites with the Mississippi between Wabasha and Winona but its small discharge has little effect on the main stream. Below Lake Pepin the river is a stream of many channels and sloughs with a bed of sand, gravel, and fine silt.

TABLE II. *Average Monthly Stream Flow; Cubic Feet Per Second; 1928*

	Mississippi at Lock and Dam	Minnesota at Mouth	Mississippi at St. Paul	St. Croix at Mouth	Cannon at Mouth	Chippewa at Mouth
January	2,375	227	2,610	2,290	121	5,337
February	2,750	2,825	5,060	2,290	578	5,554
March	7,940	6,317	13,300	7,919	522	13,294
April	10,850	3,955	17,500	13,043	680	21,585
May	6,730	2,373	11,300	7,638	680	12,646
June	4,930	396	5,780	3,860	179	6,926
July	5,790	227	6,470	5,326	80	4,959
August	5,640	1,469	7,410	3,368	336	4,754
September	8,532	1,243	10,500	6,773	227	11,766
October	10,600	500	11,100	7,101	173	12,639
November	6,730	660	7,390	4,696	127	6,890
December	4,400	210	4,610	3,245	97	5,648

HYDROMETRIC DATA

The upper Mississippi watershed has extensive and artificial storage basins by means of which the summer flow of the river is regulated and maintained in the interest of navigation. Since data relative to stream-flow records, stages of the river, and other hydrographic conditions have recently been compiled and discussed by Galtsoff (1924) and by the Metropolitan Drainage Commission in their report of 1928, it appears sufficient merely to present records covering the period of this investigation. Monthly averages of stream-flow records at several points on the watershed are presented in Table II.

The averages for the Mississippi River at the Twin City Lock and Dam and at St. Paul are taken from the actual gauging station records at those points. There are no records available for the discharges at the mouths of the various tributaries since the gauging stations on these rivers are all sit-

uated at some distance above the mouth. The tabular mean discharges at the mouth of each tributary are computed values which were obtained by multiplying the mean, as given in the station records, by the ratio of the total drainage area of the tributary to the drainage area above the gauging station.

In much the same manner it was possible to calculate the approximate mean discharge of the Mississippi at various points along the river. This was done in order to determine the ratio between the tributary discharges and the discharges of the main river at the confluence of these streams. By this process it was calculated that addition of the tributary waters increased the stream flow of the Mississippi during 1928 by the following percentages:

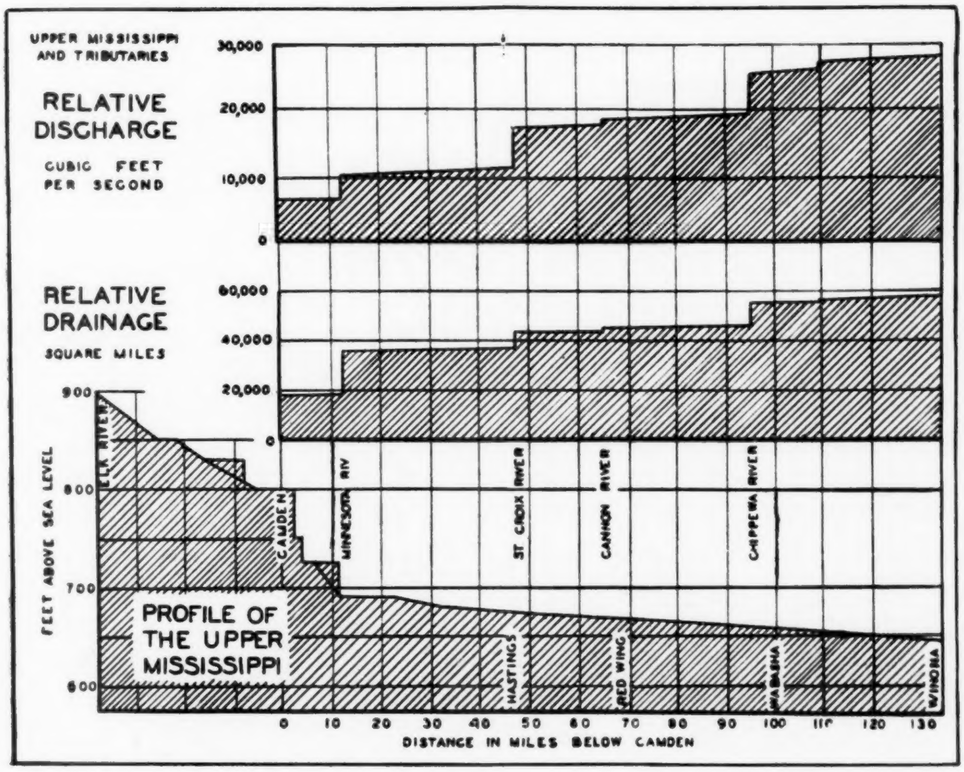


FIG. 2

The Minnesota added 18% to the volume of the Mississippi
The St. Croix added 39% to the volume of the Mississippi
The Cannon added 2% to the volume of the Mississippi
The Chippewa added 63% to the volume of the Missisippi

There is a great disparity between the relative drainage areas of these tributaries and their relative discharges as shown graphically in Fig. 2. This is attributable to the difference in run-off and to some extent to the difference in rainfall between the various watershed areas. This chart, however, does not represent stream flow conditions as they existed in 1928; it pictures the average condition of the streams over a period of years.

METEOROLOGICAL DATA

The position of Minnesota gives it a climate that is largely continental, one in which the temperature extremes are great and the humidity and rainfall moderate. The mean summer temperature of the state is quite comparable to that of France or Germany while the mean winter temperature is similar to that of central Russia or northern Sweden. The mean annual temperature taken for a period of twenty-five years is 5.3°C. (41.5°F.). January is the coldest month with a mean temperature of -12°C. (10.5°F.) and July is the warmest month with an average temperature of 21.1°C. (69.3°F.). The average annual precipitation of the state for a period of 75 years is 29.03 inches; the average number of clear sunshiny days for a period of twenty years is 148, partly cloudy days is 110, and cloudy days 107.

The water temperature of the Mississippi River taken in the channel varied during the period of investigation from approximately 0°C. in the winter to a maximum of 30°C. in the summer. There is little difference between the surface and bottom temperatures of the river. The temperature difference is usually less than 1°C. during the summer according to Galtsoff (1924). In Lake Pepin, a shallow lake not characterized by the presence of a thermocline, the maximum difference between surface and bottom temperatures observed by Galtsoff was 6.5°C. but the difference between the temperatures at the 1.5 m. stratum and the bottom was only 0.9°C.

The portion of the river discussed in this paper flows through a region which is included within the Transition Zone as defined by Merriam, but the southerly course of the river, the influence of the Twin City area, Lake Pepin, and other factors operate to produce within a comparatively short range of miles noticeable temperature differences which can best be realized by a study of Table III. The data for 1926-27 are taken from the records of H. R. Crohurst, who collected samples from each station on an average of four times a week. The data for 1928-29 are compiled from the records of the Minnesota State Board of Health and the Metropolitan Drainage Commission, and are based on an average of fortnightly readings in 1928 and weekly readings in 1929.

This table illustrates two points: (1) The discharge of sewage and heated industrial wastes combined with warmth produced by organic decomposition brings about a rise in temperature as the water passes through the metropolitan district. (2) Lake Pepin has the temperature characteristics of a true lake. In spring the water of the lake is cooler than that of the inflowing river but in the fall it is warmer since the lake is large enough to retain the summer heat for a comparatively long time.

ANALYTICAL DATA

Since knowledge of the chemical factors is useful in interpreting biological data from the same sources, a brief summary and discussion of the analytical

results are included here. It may not be out of place first of all to give the meaning of the various physical and chemical determinations and the procedures which were followed in laboratory analysis.

Turbidity is a measure of suspended matter which obstructs the passage of light. Water may be turbid due to silt, clay, suspended iron, organic matter, micro-organisms, etc. The turbidities of the samples in this investigation were measured by comparison with silica standards according to the procedures defined by the United States Geological Survey.

TABLE III. *Average Monthly Water Temperatures of the Mississippi River (Degrees Centigrade)*

Miles below Camden	0	10	28	45	68	95	100	131
	Camden	Lock and Dam	Inver Grove	Above Hastings	Above Red Wing	Outlet of Lake Pepin	Below Wabasha	Above Winona
1926–27								
Jan.	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+		0.0+
Feb.	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+		0.0+
Mar.	1.0	1.2	1.2	2.5	1.9	1.4		2.2
Apr.	7.2	7.4	7.8	7.6	7.3	6.9		7.4
May	12.8	12.7	13.3	14.5	14.8	13.6		12.0
June	18.4	19.0	18.9	18.9	18.3	18.1		18.8
July	22.7	23.6	23.1	23.8	22.8	22.6		22.0
Aug.	20.9	21.6	21.3	22.3	21.8	22.0		23.3
Sept.	16.4	16.9	16.4	17.4	18.7	19.3		21.7
Oct.	9.5	9.8	9.8	11.7	10.4	13.9		13.0
Nov.	1.4	1.6	1.4	2.8	1.0	3.5		3.2
Dec.	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+		0.0+
1928–29								
Jan.	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+
Feb.	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+
Mar.	0.0+	0.0+	0.0+	2.0	2.0	1.0	1.0	1.5
Apr.	5.0	5.5	6.5	8.0	6.0	4.4	5.5	4.0
May	7.5	8.5	9.0	19.0	18.5	17.0	16.0	20.0
June	17.8	18.3	19.0	22.3	21.5	20.0	19.0	18.5
July	23.9	25.3	25.3	24.3	23.8	22.3	22.5	23.0
Aug.	22.3	23.1	22.9	22.7	23.3	22.9	22.0	22.7
Sept.	14.9	16.0	16.3	16.5	17.5	17.5	16.3	16.5
Oct.	11.6	12.0	12.8	11.8	11.8	13.3	13.0	15.0
Nov.	2.0	2.6	2.8	3.8	3.8	4.3	5.0	6.0
Dec.	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+	0.0+

Color is principally imparted to water by dissolved or colloidal substances of vegetable origin but it may also be due to iron and manganese. Determinations of color were made by comparison with platinum-cobalt standards.

Total Hardness is expressed in terms of the calcium carbonate equivalent of the calcium and magnesium salts present. It was ascertained by calculation from the calcium and magnesium content of the water.

Alkalinity is a measure of the carbonates and bicarbonates, and is included in the hardness determination. Results are expressed as parts per mil-

lion of calcium carbonate. The determination was made by the titration method with methyl orange as the indicator.

Hydrogen-ion Concentration was measured by colorimetric methods.

Chlorides in water may be derived from mineral deposits as well as from polluting materials like sewage and industrial wastes. Titration was the method of determination.

Dissolved Oxygen is expressed in parts per million. The solubility of oxygen in water varies with temperature, so for some purposes the amount of dissolved oxygen is expressed in per cent of saturation. The Rideal-Stewart modification of the Winkler method was employed in making the oxygen tests.

Bio-chemical Oxygen Demand of polluted water is the oxygen in parts per million required during stabilization of its organic matter by aerobic bacterial action. The complete demand is usually satisfied in 20 days at 20°C., but in practice shorter periods of incubation are used. The initial oxygen content of the sample minus the oxygen content after incubation gives the demand or consumption in parts per million for the stated number of days incubation. This demand was calculated by the dilution method.

The chemical procedures in all the above examinations are those described in the sixth edition of "Standard Methods of Water Analysis," a publication of the American Public Health Association. Determinations of temperature, of hydrogen-ion concentration and of dissolved oxygen were made in the field. All other examinations were carried on in the laboratory.

The water of the Mississippi River is consistently turbid throughout the year but never does it reach the high turbidities of the smaller tributaries. Turbidities vary with the river heights, the peaks of turbidity coming at times of high run-off and heavy floods. The river at the outlet of Lake Pepin was low in turbidity on all occasions. This indicates that the lake acts as a settling basin, producing clarification as the velocity of the current is reduced. In mineral content the river presents distinct characteristics. It is mainly a calcium carbonate water, as is shown by the high alkalinity and hardness. The water is softer than that of the Minnesota or the Cannon and harder than the water of the St. Croix and Chippewa rivers. From Camden to Hastings there is a progressive increase in mineral content. At Red Wing and Wabasha the diluting effects of the soft-water Wisconsin tributaries are noticeable in the decreased values at those stations.

The chlorides appear to be due mainly to sewage contamination. They increase proportionally with the pollution and decrease with the progress of purification and recovery.

The oxygen conditions are shown graphically in Fig. 3, which also illustrates the reaeration produced by the St. Anthony Falls and the effect of the tributaries. Lake Pepin acts in a dual rôle. In summer the oxygen supply of the river is greatly increased by passing through Lake Pepin as a result

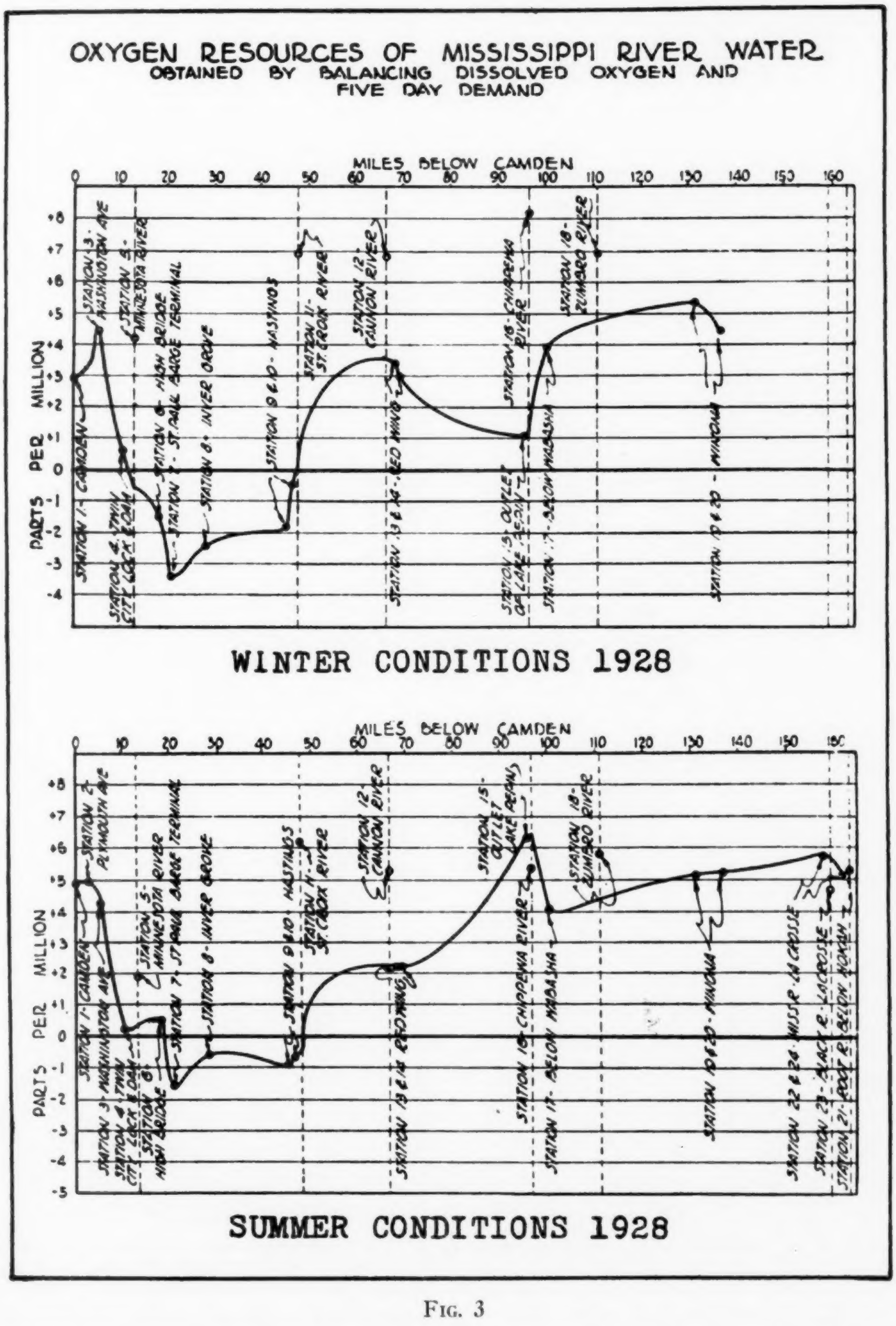


FIG. 3

of the photosynthesis and the wind and wave action on the broad surface of the lake. But in winter, when the ice-cover prevents absorption of oxygen from the atmosphere, the dissolved oxygen is considerably reduced because

TABLE IV. *Summary of Physical, Chemical, Bio-Chemical and Bacteriological Analyses for all Plankton Stations on the Mississippi River, 1928*

Station	Location	Color			Turbidity			Total Hardness			Alkalinity			Chlorides		
		Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.
1	Camden Ave. Bridge	...	..	..	70	5	13	203	108	137	209	99	145	14	2.8	6.56
4	Lock and Dam, Mpls.	...	..	..	65	6	15	218	108	140	200	108	146	18.7	5.5	10.5
8	Inver Grove	...	..	..	120	10	39	218	124	172	210	114	155	34.2	7.6	15.5
9	Above Hastings	120	27	51	60	4	23	253	138	180	243	115	159	16.5	1.0	5.5
13	Above Red Wing	100	15	53	240	0	24	190	103	148	185	101	131	9.0	0.5	3.0
15	Outlet of Lake Pepin	75	20	45	10	0	5	198	120	151	193	105	135	9.0	0.0	3.3
17	Below Wabasha	90	13	53	200	2	17	172	80	123	179	60	110	7.0	0.0	1.9
19	Above Winona	110	36	64	135	0	26	156	40	111	139	45	100	4.5	0.0	1.3

Station	pH Value			Dissolved Oxygen			5-Day Demand			Bacteria per c.c., 37° C., 48 hrs.			*B. coli* per c.c.		
	Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.
1	8.0	7.4	7.86	11.6	4.1	8.2	6.6	0.7	2.4	11,500	80	1,726	100	0.1	11
4	8.4	7.4	7.8	12.7	2.9	6.8	8.4	2.2	4.2	830,000	5,700	193,257	10,000	10	1,591
8	8.0	7.5	7.8	11.5	2.3	6.7	14.0	3.1	6.0	1,000,000	8,900	156,924	10,000	100	2,071
9	8.0	7.5	7.7	11.1	1.5	5.8	11.1	1.3	5.0	220,000	3,900	60,345	1,000	10	545
13	8.1	6.5	7.65	10.5	2.6	6.3	4.5	1.5	2.7	93,000	475	21,659	1,000	10	159
15	8.4	7.3	7.9	11.9	3.7	7.3	4.7	1.1	2.2	3,100	41	643	10	0.02	1
17	8.4	7.2	7.8	11.3	4.1	7.2	3.9	0.6	1.7	7,700	55	1,408	10	0.1	5
19	8.4	7.2	7.7	11.7	6.6	8.2	5.1	1.1	2.3	21,500	150	2,712	100	1	14

of the large amount of organic matter which the river deposits in this great settling-basin.

Table IV gives a summary of the analytical results obtained from a study of 21 samples of water collected at each station on the Mississippi River.

POLLUTION ZONES

Information obtained by the Minnesota State Board of Health and cooperating departments indicates that the Mississippi River may be roughly divided into the following zones according to the degree of pollution:

Zone 1. A zone of heavy pollution extending from Minneapolis to the junction with the St. Croix River. Water in this zone is unfit for use as a source of water supply and is a potential danger from a health standpoint to persons and livestock coming in contact with it. Nuisances are frequent and fish life has been practically exterminated in this area.

Zone 2. A zone of partial recovery extending from the junction with the St. Croix River to the head of Lake Pepin. Conditions are somewhat improved over Zone 1 as a result of the dilution effected by the addition of water from the St. Croix and the natural process of stream purification. The river is unfit for use as a source of water supply, but nuisances are less frequent and fish life is less restricted than in Zone 1.

Zone 3. A zone of more complete recovery extending through Lake Pepin. By the time the outlet of the lake is reached, the water meets the bacterial standards for permissible loading of water-purification plants.

Zone 4. A zone of intermittent pollution and recovery below Lake Pepin. The water below Lake Pepin appears to have practically recovered from the pollution introduced above the lake, and the pollution in this zone is local below each municipality.

THE MINNESOTA RIVER

Although the source of the Minnesota River is on the eastern slope of the Dakota foothills in South Dakota, it does not become a permanent stream until it emerges from Bigstone Lake at Ortonville in Bigstone County, Minn. Here, uniting with the Whetstone River, it flows southeastward to Mankato, then turns sharply and flows northeastward to its junction with the Mississippi at Fort Snelling, just below the Twin City Lock and Dam in the Metropolitan area. Throughout this portion of its course it has a wide valley with the bottom lands marshy especially from Chaska to the mouth, a distance of thirty miles. The drainage area is almost entirely prairie or cultivated land. The mean slope of the Minnesota River, excluding the portion above Bigstone Lake, is considerably less than that of the upper Mississippi River. During the last fifty miles of its course the river is very nearly level. The rainfall in the drainage area is about 26 inches, but since the run-off is comparatively slight, the discharge of the river is not as great as that of the St. Croix or the Chippewa Rivers, which drain areas much smaller in size.

It is evident from the bacteriological and chemical results that the Minne-

sota River is not a clean stream. Sewage and industrial wastes combine to give a population equivalent which is estimated at 100,000. This pollution makes itself evident in the fairly high oxygen demand, the excess of chlorides, and the bacteriological counts which exceed those of the other tributaries considered in this paper. In other respects the quality of the water is marked by a high mineral content due to the influence of the cretaceous formations in the valley, and a moderate amount of color and considerable turbidity which are characteristic of prairie streams.

THE CANNON RIVER

The Cannon River which enters the Mississippi a short distance above Red Wing is a small tributary rising in Shields Lake in the western part of Rice County, Minn. Its meandering course takes it through a chain of seven lakes, the last of which is Cannon Lake, a large body of water several miles in area located 60 miles from the mouth. Above that point the drainage basin contains at least twenty-five lakes. Its chief tributaries are the Little Cannon and the Straight Rivers.

TABLE V. *Physical, Chemical, and Bacteriological Analyses of Water at Station No. 5, Minnesota River at Fort Snelling. Summary of 21 Samples; January-December, 1928*

Determination	Maximum	Minimum	Average
Color	...	...	...
Turbidity – p.p.m.	180	10	75
Total Hardness – p.p.m.	368	155	263
Methyl Orange Alkalinity – p.p.m.	318	108	197
Chlorides – p.p.m.	18.2	1.8	6.8
Hydrogen-ion Concentration	8.3	7.5	8.0
Dissolved Oxygen – p.p.m.	13.8	3.9	8.0
Per Cent Saturation	117.5	37.5	69
5-Day Biochemical Oxygen Demand	7.0	1.2	3.5
Bacteria per c. c., 37° C., 48 hours	28,000	320	7,260
B. coli per c.c.	1,000	1	63

Throughout its length the Cannon River has considerable fall. From Faribault to the mouth, a distance of 59 miles, the river has an average slope of 4.9 feet per mile. The valley is in general narrow and steep-sided so that the rainfall, which averages 30 inches in the lower part of the basin, quickly reaches the stream causing sudden rises and giving the river a flashy character. Except for these sudden floods the flow of the Cannon is very uniform but its discharge is comparatively so small that it has little influence on the Mississippi River.

In chemical characteristics the Cannon resembles the Minnesota River. Like the latter it lies in a basin which is similar in geological structure and is given over to extensive cultivation. The population equivalent of the combined pollution from sewage and industrial wastes is estimated at 22,800. The heavy fall of the river and its consequent rapid current produces a well

aerated condition of the water which makes the Cannon River rank highest among all the stations in dissolved oxygen content of the water and average per cent saturation.

THE ST. CROIX RIVER

The drainage basin of the St. Croix River lies in eastern Minnesota and northwestern Wisconsin, and the river throughout the greater part of its length forms the boundary between these two states. From its head-waters on the Lake Superior divide the St. Croix River flows southwest and then south until it joins the Mississippi opposite Hastings, Minn. The lower part of the drainage basin is largely under cultivation but the upper section is timbered. Glacial drifts cover almost the entire basin so that outcrops of rock are infrequent and limited in extent. The exposed outcrops are mostly hard igneous formations. Sedimentary formations are relatively few.

TABLE VI. *Physical, Chemical, and Bacteriological Analyses of Water at Station No. 12, Cannon River at Red Wing. January-December, 1928. Summary of 21 Samples*

Determination	Maximum	Minimum	Average
Color	70	15	32
Turbidity – p.p.m.	4,000	2	205
Total Hardness – p.p.m.	263	145	205
Methyl Orange Alkalinity – p.p.m.	236	121	179
Chlorides – p.p.m.	7.0	1.0	4.0
Hydrogen-ion Concentration	8.4	7.6	8.0
Dissolved Oxygen – p.p.m.	13.2	5.3	9.5
Per Cent Saturation	109	71	87
5-Day Biochemical Oxygen Demand	7.2	0.43	2.6
Bacteria per c.c., 37° C., 48 hours	48,000	230	6,086
B. coli per c.c.	100	0.1	12.1

A heavy rainfall averaging 31 inches annually combined with a high run-off gives the river a relatively strong discharge. The grade in the upper portion from the source to Taylor's Falls is rather steep but in the last fifty miles of the river's course the slope is only 0.3 foot per mile. One mile above Stillwater the river spreads out to form a lake one-half mile to one mile in width and six to fifteen feet deep which continues for twenty-five miles to Prescott. Here the lake narrows abruptly and connects with the Mississippi through a short channel. Lake St. Croix owes its origin to the alluvial deposits of the Mississippi which obstructed the mouth of the tributary and caused it to fill out its valley.

St. Croix River flows for the most part between high bluffs of gravel or of rock. Consequently the water is very low in turbidity although it is highly colored by woodland drainage. The water of the St. Croix possesses the quality of softness and low alkalinity which are associated with the geological characters of the drainage area. By reason of the high discharge and the considerable quantity of oxygen which it carries, this tributary exerts a purifying influence on the Mississippi. According to all the parameters by which

we measure the sanitary quality of water, St. Croix River at the mouth is a clean stream, surpassing all other localities which were examined in the course of this investigation.

TABLE VII. *Physical, Chemical, and Bacteriological Analyses of Water at Station No. 11, St. Croix River at Prescott. Summary of 21 Samples; January-December, 1928*

Determination	Maximum	Minimum	Average
Color	130	20	71
Turbidity – p.p.m.	17	0	4
Total Hardness – p.p.m.	141	48	85
Methyl Orange Alkalinity – p.p.m.	194	48	84
Chlorides – p.p.m.	2.0	0	0.3
Hydrogen-ion Concentration	8.4	7.2	7.6
Dissolved Oxygen – p.p.m.	11.6	4.35	8.0
Per Cent Saturation	109.5	48.5	73.5
5-Day Biochemical Oxygen Demand	3.1	0.4	1.3
Bacteria per c.c., 37° C., 48 hours	8,000	42	1,118
B. coli per c.c.	10.0	0.02	1.4

THE CHIPPEWA RIVER

The Chippewa River, which enters the Mississippi opposite Reads Landing, has its origin in more than a hundred lakes, large and small, and many connecting swamps lying in northwestern Wisconsin near the Michigan boundary. The upper Chippewa and the Flambeau rivers unite 112 miles from the mouth to form the Chippewa proper. About half of the total drainage area includes the least settled part of northern Wisconsin. Above Chippewa Falls the drainage basin is covered with glacial drift, and the underlying crystalline rocks appear only in the river bed. The river in the southern part of its course has a slope of 2.3 feet per mile extending to Chippewa Falls, 62 miles above the mouth. The mean annual rainfall in the catchment area is about 30 inches, and the river discharge is greater than that of any other tributary from Minneapolis to the Iowa line.

TABLE VIII. *Physical, Chemical, and Bacteriological Analyses of Water at Station No. 16, Chippewa River, Opposite Reads Landing. Summary of 21 Samples; January-December, 1928*

Determination	Maximum	Minimum	Average
Color	140	40	76.9
Turbidity – p.p.m.	700	3	44.2
Total Hardness – p.p.m.	85	5	51.6
Methyl Orange Alkalinity – p.p.m.	75	20	48.2
Chlorides – p.p.m.	1	0.0	0.1
Hydrogen-ion Concentration	8.1	6.9	7.5
Dissolved Oxygen – p.p.m.	11.8	6.3	8.9
Per Cent Saturation	108	65	82
5-Day Biochemical Oxygen Demand	3.7	0.8	2.1
Bacteria per c.c., 37° C., 48 hours	18,500	150	3,914
B. coli per c.c.	100	0.1	22.0

The Chippewa River has not the flashy character of the Cannon, but in flood time the water becomes very turbid. Its high color and low mineral content reflect the topographical features of the watershed, while the hydrogen-ion value, lower on the average than that of the Mississippi or its other tributaries, in this region, is a natural consequence of swamp drainage, low alkalinity and trade wastes from various sources of pollution.

METHODS OF SECURING BIOLOGICAL DATA

Sampling Devices

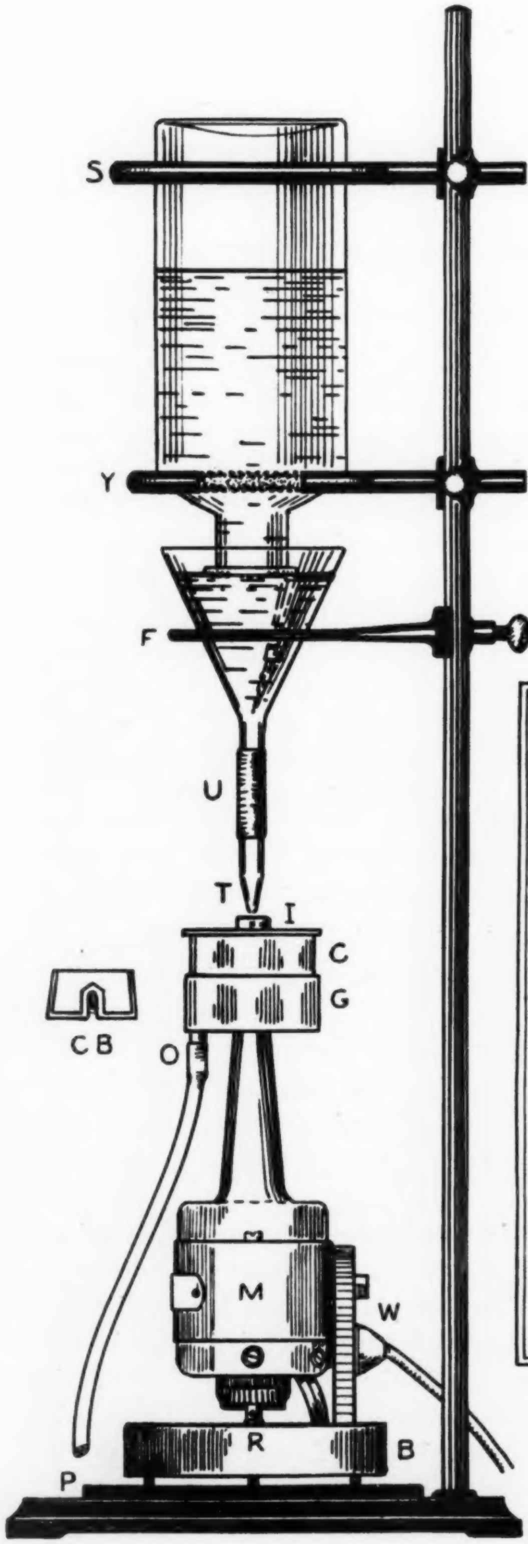
By means of a sampler designed especially for the work, it was possible to collect simultaneously samples of water for all the various analyses and thereby insure comparative results. This sampler was similar to the one used by the United States Public Health Service in its studies on the Illinois River, and consisted of a pail containing a rack for holding several bottles, which were filled through separate glass tubes fitted into thimbles in the cover of the pail by means of one-hole stoppers. The samples of water for plankton enumeration were therefore obtained concurrently with the samples for chemical, physical, and bacteriological analyses. In all cases the pail was lowered in mid-stream and the sample secured at an approximate depth of five feet below the surface. Two liters of water was the amount collected for plankton examinations. The immediate addition of formalin preserved the sample, which was then shipped to the laboratory for centrifuging and study.

The Centrifuge

The small electric centrifuge designed by Mr. J. P. Foerst of the University of Wisconsin and described by Juday in his "Third Report on Limnological Apparatus," 1926, was employed throughout this investigation to obtain the concentrated plankton material from the water. This machine was operated at the maximum speed of 20,000 revolutions per minute.

The Wisconsin limnologists fed the water into the centrifuge from a one-liter aspirator bottle which was placed on a box beside the centrifuge, the rate of flow being regulated by a glass stop-cock in the outlet of the tube of the aspirator bottle. It was found that for most efficient operation the water should run through at a rate of one liter in 6 or 7 minutes. Instead of using this method, we devised another arrangement (Fig. 4) based on the principles of a self-feeding "drinking fountain." The sample of water is run directly into the centrifuge from the original collection bottle, which is inverted over a glass funnel fitted with a special tip to control the proper rate of flow. A bit of glass tubing drawn out to a point which allows a discharge of approximately two liters in 15 minutes may be attached to the funnel to regulate the flow or the tip of the funnel itself may be narrowed to the proper aperture.

The funnel is set in a ring fastened above the bowl of the centrifuge.



SKETCH OF FOERST ELECTRIC CENTRIFUGE AND IMPROVED FEEDING APPARATUS

P, pad, rubber or felt;

B, base; M, motor;

R, rheostat; W, motor terminals;

G, guard; C, cover;

CB, cross section of bowl;

I, inlet tube; O, outlet tube;

T, tip regulating flow;

U, rubber tubing;

F, funnel support;

Y, incomplete ring for bottle support;

S, guard ring.

FIG. 4

Another ring above the funnel forms a support for the neck of the inverted sample bottle. This ring may be cut into a C-shape to facilitate inversion of the filled bottle. The supports for funnel and bottle are clamped to an iron bar which is bent at double right angles and fastened to the wall. For portable use a ring-stand may be substituted as shown in the illustration. A heavy pad of rubber or felt placed beneath the centrifuge reduces the noise made by the machine. As the water leaves the funnel more water is automatically drawn from the reservoir above. The rising bubbles of air keep the sample agitated and prevent the plankton from settling along the sides of the container.

EFFICIENCY OF THE CENTRIFUGE

Juday tested the efficiency of the Foerst centrifuge and found that with the exception of Aphanizomenon it removes approximately 98% of the organisms that are usually considered in a plankton catch. Only about half of the actual amount of Aphanizomenon in the sample was removed in the first centrifuging but substantially all could be removed by a second centrifuging. It appears that other *Myxophyceae* that are lighter than the water may also be troublesome in this respect.

The limitations of the centrifuge were not realized until the Mississippi investigation was well under way, and it was too late to correct for these sources of error. But since the Foerst centrifuge has, all in all, a very high efficiency and since according to Juday (1926) plate counts have shown that even 40 to 70 per cent of the bacteria are removed from the water by the first centrifuging, it seems unnecessary for ordinary purposes to submit the sample to a second passage through the machine.

METHODS OF COUNTING

The actual examination of the plankton consisted of a qualitative enumeration to determine the kind of organisms present, and a quantitative estimate of the bulk or volume of each species as well as of the actual number of individuals. The volumetric unit is a cube with linear dimensions of 20 microns, known as "The Cubic Standard Unit." Its volume is 20 x 20 x 20, or 8,000 cubic microns. The volumetric values obtained in the plankton count have been expressed in cubic standard units per cc. of unconcentrated water. For comparison of actual numbers, results are given in number of individuals per liter of water. Limnologists, it is true, generally calculate the number of organisms per cubic meter of water. This is logical with the net-method or when large samples of water are used for centrifuging, but it seems like fictitious accuracy to estimate the population of a cubic meter when only .002 or 1/500 part of that unit is collected for examination as in this case.

An ordinary Sedgewick-Rafter cell and a Whipple micrometer eye-piece were employed in making the enumerations. Under the low power objective

every portion of the counting cell was first examined to enumerate the uncommon and larger organisms. These were noted individually and recorded on the counting sheet in the column headed "Survey Count." Then five fields, each having an area of one cubic millimeter, were selected for the enumeration of the nannoplankton. By using separate factors for survey count and for the field count, the results could be expressed in terms of 1 cc. of water or calculated per liter if desired. The simplest field-count formula applicable to the methods outlined is the following:

$$\frac{\dfrac{\text{Volume of Concentrated Sample in Cubic Centimeters}}{\text{Volume of Original Sample in cc.}}}{} \times \frac{\text{Capacity of Counting Cell in Cubic Millimeters}}{\text{Number of Fields Counted}} = 1 \text{ cc. Factor}$$

Since in the survey as many fields are counted as there are cubic millimeters in the counting cell, the factor for expressing survey values in terms of a cubic centimeter is obtained by the use of the first fraction alone. Thus if 2,000 cc. are concentrated to 20 cc. and five fields are counted, the factor is 2 for the total field count and .01 for the survey count. The volumetric system of counting in cubic standard units is well explained in the fourth edition (1927) of the "Microscopy of Drinking Water" by Fair and Whipple.

PART II

INFLUENCE OF PHYSICAL, CHEMICAL, AND BIOTIC FACTORS

INFLUENCE OF PHYSICAL CONDITIONS ON THE PLANKTON

The factors that influence the plankton life of a stream may be roughly divided into three categories: physical, chemical, and biotic. The physical conditions of life in stream or lotic environments are more severe than those which are associated with life in limnetic habitats. The instability of the river, its fluctuating levels, its changing velocity and turbidity; these affect the plankton most profoundly (Kofoid 1908). The intrinsic physical factors such as velocity of the current, transparency of the water, amount of silt and of suspended solids are bound up very closely with the changing hydrograph. A rise in water levels is accompanied by a rise in turbidity, diminished transparency, and increased velocity. The hydrograph then is one of the key indicators required for the explanation of the plankton data. The temperature of the water and the amount of sunlight are also among the more important factors.

Physical conditions alone do not tell the whole story of the relation of the environment to the growth and decline of the organisms but in rheology the character and fluctuations of the plankton are better understood in relation to physical than to chemical or biotic conditions. A graph (Fig. 5) has been prepared in which the volume per cubic centimeter of total plankton in the Mississippi River at Inver Grove is plotted by dates of collection and contrasted with the various physical factors of the environment. The daily river heights at the Robert Street Gauging Station in St. Paul were used to form the hydrographic record. The relative mean cloudiness (United States Weather Bureau observations at St. Paul) is used as an index of the relative amount of sunlight from month to month. The turbidity and temperature records are of the water at the place and time of plankton sampling.

The peaks and troughs in the plankton curve are all understandable if analyzed in accordance with one or more of these physical factors. Thus at one time a sharp rise in river levels depresses the plankton curve most severely, at another time it may be the extreme cloudiness or the turbidity which checks the plankton. The greatest plankton pulses, as shown by this graph, occur only at times when all physical conditions are favorable. No single factor will explain the planktonograph, but the combination of these does offer a reasonable explanation of the major variations in the abundance of plankton organisms.

Plankton literature is rich in suggestions of various factors which might explain the periodicity in the multiplication of the individual organisms and

the varying amounts of plankton from one week to the next. These suggestions range from food-stuffs to lunar cycles and each in turn is supported by evidence which demonstrates some relationship between the factors advanced and the plankton (Apstein, 1896; Kofoid, 1908; and others).

Liebig's "Law of the Minimum" precludes the possibility of a single food-substance being responsible for plant growth. A certain number of substances are required and each of these must be present in certain minimal amounts. If one of these is absent, no matter how abundant the others may be, the plant dies. An extension of this law to include other environmental conditions besides food-stuffs is in my opinion the key to the fluctuations and to some extent to the periodicity of the plankton. No matter how favor-

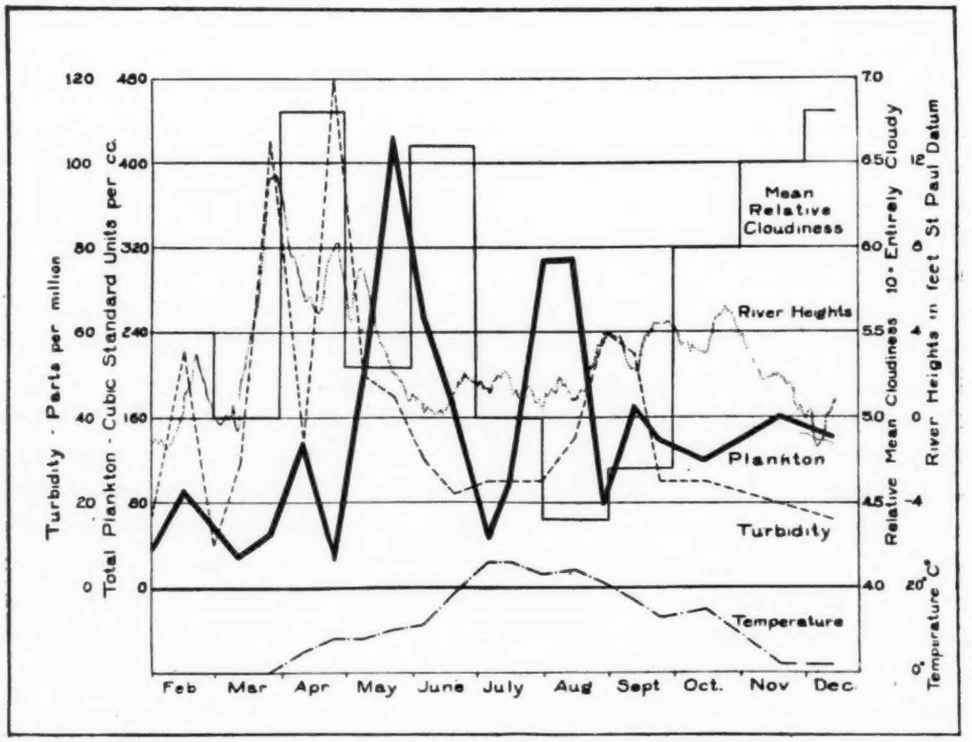


FIG. 5

able the food elements or the sunlight or other factors may be, a single adverse physical condition may wipe out the organisms or reduce their development to a minimum. Conversely, should all physical factors be at an optimum for plankton development and one indispensable food element be lacking, the plankton will not profit.

A somewhat similar idea is expressed by Wundsch (1920) in the law which he calls "Gesetz von der Augenfälligkeit des inkonstanten Faktors." Wundsch states that when several factors of similar effectiveness are operating simultaneously, that factor produces the most conspicuous biological effect for the time being which exhibits the greatest fluctuations, provided

that the other more constant factors continue to satisfy the minimal demands of the organisms. For instance, if nutritional factors were constant and near the optimum, one would find a parallelism between the temperature curve and the plankton curve. Conversely, if temperature were constant and in the optimum range while the quantity of food substances changed markedly, the fluctuations of nutritional factors would impress themselves upon the curve of plankton production. Utermöhl (1926) has the same viewpoint but expresses it more briefly and precisely: "Die quantitative Entwicklung eines Organismenbestandes wird durch denjenigen der notwendigen äusseren Faktoren bedingt, dessen Intensität im Vergleich mit den übrigen Faktoren ein Minimum darstellt."

We are so accustomed to think of plankton phenomena in terms of dissolved organic and inorganic substances because most of our knowledge of plankton biology comes from investigations of the ocean and of fresh-water lakes. Comparatively little has been done to investigate the conditions which affect the plankton crops of rivers and streams. Enough work has been done, however, to bring out the major rôle that physical conditions play in the ecology of river plankton. The age of the water, the slope of the river, and hydrographic stability are all phases of the same general type of physical influence. If all these influences are weighed, the most important place must be given to *current* in all its various implications, for after all the current is the distinguishing characteristic of lotic environments.

It was Schröder (1899) who, as a result of his work on the phytoplankton of the Oder River, proposed the theory that the amount of plankton in a river is in inverse proportion to the slope of that river. This statement is not of universal application since there are other conditions besides the slope of the river that determine plankton productivity but the idea deserves further analysis and comment. The velocity of the current, as already suggested, is one of the main limiting factors in plankton production, and many investigators have pointed out that rich plankton crops coming from the upper part of a river may be destroyed by passing through a series of rapids or sharp falls and that stream velocities may assume destructive proportions. Kofoid (1903, 1908) on the basis of his five-year study of the Illinois River came to the conclusion that:

> "The age of the water is an important factor in the production of plankton in streams. Young streams have but few plankton. Impounded for 10 to 30 days this barren water develops an abundant plankton crop. The rate of run-off and replacement of impounded waters influences plankton production, being greatest where run-off and renewal are least."

Analyzing and combining these various ideas, it may be stated that the environment which allows the greatest time for the development of plankton will produce the greatest crop. A swift stream allows little time per unit of distance. A sluggish stream allows much greater time. The longer the time

during which organisms may remain in their moving habitat the greater will the opportunities for their development be. This general proposition like most other statements in rheology may meet with many exceptions. A long river such as the Mississippi is affected by diverse local conditions that counteract the tendency towards increased productivity. As the Mississippi increases in size and its waters age, it also becomes more turbid and changed in character by inflowing tributaries so that the normal regimen of plankton production may be interfered with. Nevertheless it may be said that if other conditions are equal, the productivity of a stream is proportionate to the age of its water and inversely proportionate to its velocity.

The velocity of a stream has another effect upon the plankton, which has often been commented on, especially by Kofoid, who repeatedly remarked that the addition of adventitious organisms to the plankton was mainly associated with floods and increased velocity. I have noticed that adventitious plankton organisms, diatoms in the main, are more frequently encountered during winter than at other seasons. This observation, I believe, can be correlated with the effect of ice cover on the distribution of stream velocities in the vertical.

The whole subject of the nature of the stream flow of rivers is well explained in the volume "Stream Gauging" (1927) by W. A. Liddell from whom I shall quote the following:

"The distribution of velocities in a vertical for open water conditions follows a parabolic law, the actual values of velocities at the different points in the vertical being affected by the resistance to flow met with by the water at the different depths. The maximum velocity occurs generally in the upper third; the surface velocity depends upon the width and depth of the channel and roughness of the bed and sides; and the bed velocity depends on the roughness of the bed. With ice cover formed, the same controlling factors are present except that the air surface is replaced by ice surface. The ice surface being rougher than air, the surface velocity is reduced. This causes a readjustment of velocities throughout the vertical.

"From the studies carried on by Barrows and Horton, it was found that the vertical velocity curve for ice cover was drawn back in its upper portion on account of the greater retarding effect of ice over that of air. Also, the thread of maximum velocity was lowered from 0.14 depth to 0.36 depth. The bottoms of the two curves were at substantially the same position, but with a very rough ice cover, the ice resistance may effect the curvature of the lower portion of the curve as well as the upper.

"The average position of maximum velocity under ice-cover conditions was found to be at 0.37 depth below the ice, varying from 0.19 to 0.52 depth. It is lowered as the depth and velocity increase and, hence, as the stage increases. For very rough ice cover, the open water curve may be completely reversed, the slowest velocity occurring at the ice and the maximum velocity below mid-depth."

The lowering of the point of maximum velocity in such comparatively shallow streams as the upper Mississippi and its tributaries would have a

very appreciable biological effect. Even though the bed velocity were not actually increased by ice-cover conditions, the position of maximum velocity would be so close to the bottom that benthic organisms would be subjected to a stronger current than usual and would become separated from the substratum. The attached algae and bottom diatoms would also be likely to be put in suspension by the change in the velocity curve.

INFLUENCE OF CHEMICAL CONDITIONS ON THE PLANKTON

The chemical analyses which were undertaken as part of the State of Minnesota's stream pollution program were restricted mainly to standard tests that have a direct sanitary significance. These tests did not include determinations of the amount of free carbon dioxide and the various compounds of nitrogen, which would have been very useful in interpreting the plankton data. It is therefore impossible to give a thorough exposition of the chemical conditions that affected plankton life during the period of investigation.

As may be seen from the tabulated records, the dissolved oxygen was never depleted to such an extent that it would seriously interfere with plankton growth. When fish are suffocating under the ice during winter and chemical tests show that the oxygen is reduced to minimal amounts, the plankton life of the stream is still normal. During midwinter I have repeatedly observed swarms of Entomostraca swimming actively about in the water of lakes which were so devoid of oxygen that the fish population succumbed.

The oxygen conditions of the upper Mississippi and their bearing on aquatic life have been investigated and reinvestigated so many times that I feel that I can add nothing further to what has already been said on the subject. Therefore I shall limit my discussion to the influence of the chemical factors of the environment to the mineral constituents of the water.

It is obvious that the inorganic materials in solution in the water vary greatly in kind and in degree of concentration depending upon the type of soil to be found in the drainage area of the streams. These substances undoubtedly have an effect on the biota of the waters. Birge and Juday (1911, 1922), for example, in their studies of Wisconsin lakes, found that many of the soft-water lakes contained much less phytoplankton than the hard-water lakes. The greater content of bicarbonates and the greater amount of free carbon dioxide in waters of high hardness stimulates the growth of organisms (Chambers, 1912). An excess of chlorides has likewise been found to acompany larger growths of microscopic organisms (Whipple, 1927). Although chlorides may not be directly utilized by plants, the chloride determination when in excess of the normal amount of chlorides present in natural waters of the same region signifies that the water contains a relatively large mass of fertilizing substances, derived usually from sewage contamination. These fertilizing substances are useful in moderate amounts for plankton growth.

The analytical data on the waters tributary to the Mississippi show that in physical and chemical respects there is a striking difference between the tributaries on the Wisconsin side compared as a group with those on the Minnesota side. The tributaries entering the Mississippi from Minnesota are high in hardness, alkalinity, and chlorides while those entering from Wisconsin are relatively low in dissolved mineral substances. The reason for this regional difference is found in the character of the soil and the geological formations of the various drainage basins. The southern Minnesota deposits abound in limestone and other calcareous rocks while the southwestern Wisconsin formations are composed more commonly of hard igneous rocks which influence the quality of the water but slightly.

The eastern tributaries, on the other hand, have a higher color than those entering the Mississippi from the west. A high color is a characteristic effect of wood-land and swamp-land drainage. The tributaries from Wisconsin drain an area that is rather well forested and often swampy but the Minnesota streams flow through a country that is principally prairie and farm land. The turbidity likewise shows a regional difference which again can be correlated with the difference in topography between the two states. In Table IX these differences are shown in conjunction with various plankton results from the same sources.

TABLE IX. *The Tributaries from Minnesota Compared with Those from Wisconsin With Respect to the Quality of Water and the Volume of Plankton*
Average of Twenty-one Samples.

Tributaries	Color	Turbidity	Hardness	Alkalinity	Chlorides	pH Value	Cubic S. Units per c.c.		
							Diatoms	Phytoplankton	Total Plankton
From Minnesota									
Minnesota...	30	75	263	197	6.7	8.0	343	445	534
Cannon......	32	205	205	179	4.0	8.0	136	145	176
Zumbro......	29	312	184	172	2.2	8.0	...	...	...
From Wisconsin									
St. Croix.....	71	4	85	84	0.3	7.6	51	65	86
Chippewa....	77	44	51	48	0.1	7.5	137	153	160
Black........	93	21	62	56	0.6	7.6	...	...	...

Since it is well known that waters rich in lime carbonates are also rich in algae, while waters poor in carbonates and containing humic acids are poor in vegetation, it would be expected that the Minnesota tributaries should have a higher plankton content than the Wisconsin tributaries. The data presented in Table IX appear to confirm this idea. Even though the relatively high turbidities of the Minnesota streams tend to suppress plankton development by the exclusion of light and indicate that the streams are subjected to severe plankton-destroying floods, still the plankton average is higher for these tributaries than for the soft-water streams in Wisconsin. The plankton of the

Zumbro and Black Rivers was not studied over an extended period of time, accordingly no biological data are given for these streams, but it was apparent that for equivalent dates the Zumbro carried a higher percentage of plankton than did the Black River.

The Minnesota River especially contrasts very strongly in plankton content with the St. Croix. Both streams are old, geologically speaking, both have about the same slope in the lower 50 miles of river. The quite marshy borders of the Minnesota, favorable for plankton development, have a sort of counterpart in broad Lake St. Croix which extends 25 miles up the river from Prescott. Still the Minnesota produces an average volume of plankton that is more than six times greater than that produced in the St. Croix per unit volume of water.

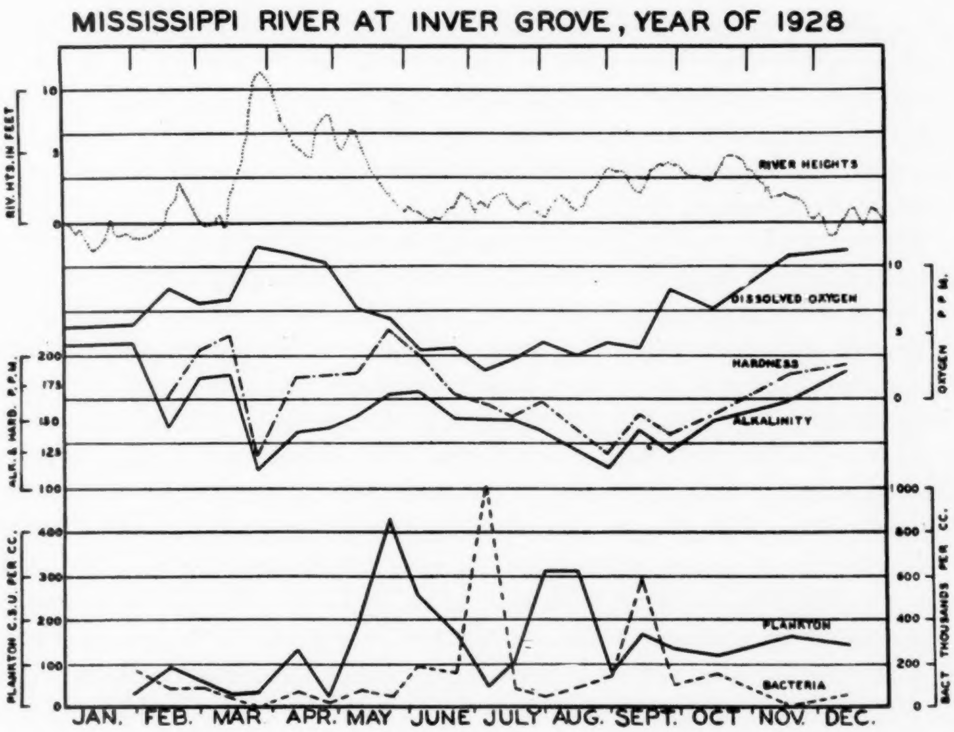


FIG. 6

Only in one group of phytoplankton organisms do the Wisconsin tributaries have an advantage over the Minnesota streams. The soft water and bog drainage of the former streams promotes the growth of desmids, which are well known to be favored by waters of such quality (Smith, 1920). The Chippewa River exceeded all other stations in the number of desmids occurring in the plankton, and these declined in number after being added to the Mississippi.

Besides comparing waters of various qualities with respect to plankton it would be interesting to find out whether the seasonal changes in the concen-

tration of mineral substances have any effect on the plankton cycle. In winter, when most of the stream flow is derived from underground water which has been in more or less contact with the mineral constituents of the ground, the inorganic substances are all present in greater amounts than at any other time of the year. The depression in hardness, alkalinity and chlorides which occurs during the season of maximum plankton development is probably due to a decrease in the supply of mineral matter at that time of the year, and need not necessarily indicate a decrease due to utilization of such substances by the plankton.

If river heights, plankton, and various chemical results are plotted together as in Fig. 6, it will be seen that the amounts of the inorganic substances vary more closely with the hydrograph than they do with the biological factors. If dilution and concentration explain the seasonal variation in the chemical quality of the water it is difficult to arrive at an estimate of the influence of these inorganic materials on the plankton cycle. A correlation between two factors may be a manifestation of cause and effect or it may be due to the fact that both factors are related in the same manner to some third factor and they vary synchronously and proportionally because they are both controlled by this same extrinsic force.

There are of course valid examples in plankton literature which show that there is a connection between the development of microscopic organisms and the amounts of certain mineral substances in the water, a connection based on the fact that an appreciable change is registered in the amount of these substances at times of maximum plankton growth. A clear-cut case of this kind is the relation between the abundance of diatoms and the silica content of the water where it is evident that the diatoms actually utilize silica to form their cell walls. Raben (1905) and Johnstone (1908) for instance have shown that the production of marine diatoms is determined by the proportion of silica in the sea water. The diatom maxima follow the maxima in the silica content of the water and the utilization of this substance by the plants causes a corresponding decrease in silica content. Pearsall (1929), as a result of his detailed studies of some English lakes, reported that diatoms were more abundant in the silted lakes than in the rocky lakes. The silted lakes have more silica in solution than the rocky lakes because more silt in suspension offers greater opportunity for the solution of silica and hence more of this substance will tend to be present in the waters. These facts suggest what may be one of the principal reasons why the diatoms are almost universally the most important constituents of river plankton. Rivers, being generally more laden with silt than are lakes, would on the basis of Pearsall's reasoning have proportionally more silica in solution than lake waters. This would favor the production of diatoms and would bring them into greater prominence in rheoplankton.

Another inorganic substance which appears to have an intimate bearing

upon plankton growth is mineral nitrogen. Recently Minder (1926) made a thorough bio-chemical study of the Lake of Zurich, and he concluded that nitrogen in the form of nitrates was the principal factor which regulated the quantity of phytoplankton.

INFLUENCE OF BIOTIC FACTORS ON THE PLANKTON

The biotic factors of the environment can not be measured quantitatively in the same manner that physical and chemical factors can. In field work it is difficult to evaluate the biotic factors and their effects on the organisms and distinguish these from the other conditions involved in environmental resistance. Biotic resistance is expressed mainly by the action of competitors, predators, and parasites. Its bearing upon plankton studies can only be hinted at in this paper. The ratio of the actual number of individuals to the potential number of individuals is a measure of the resistance of the environment. An exact application of this idea to plankton ecology is not possible in the present state of knowledge mainly because plankton deals with such a vast assemblage of organisms whose various reproductive potentials are not known with accuracy. It is possible, however, in river biology to measure the relative resistance of portions of the environment in terms of the actual numbers of organisms which enter that environment and the actual numbers which depart from it as the plankton passes through with the current.

It was significant in the present work that the plankton content of the river at some point downstream was not the sum total of the original content at Camden plus the various tributary additions. The factor of dilution did not account for the difference between the actual amount and the calculated summation of all the contributions that had been received. In cases where a sharp rise in the plankton content occurred on account of the sudden accession of tributary plankton, the river plankton quickly declined again in quantity and showed a tendency to drop back to the same level which characterized it before it received the tributary supplement. This phenomenon and its explanation may in some respects be analogous to the environmental resistance described by Chapman in the case of flour beetles cultured in a standard sized container. "If a culture is started with numbers which represent a supersaturation of the environment, the population dies down to the point of saturation. The population is limited by competition and develops an internal resistance even when all other factors of the environment are at the optimum" (Chapman, 1925).

It is a principle of ecology that the population of an environment is restricted to a saturation point determined by certain environmental conditions. Competition for food and space is the principal factor which prevents overcrowding. Pearl (1923), Chapman and others have shown that the growth curves of populations approach an asymptote which represents a condition

of saturation. Applying this to the matter at hand, it may be assumed that when tributary additions bring about a supersaturation of the plankton population the decline which follows is a return to a state of equilibrium. The plankton population curve, therefore, is a function of the main environment itself. Positive deviations from this curve brought about by additions from without have only a temporary influence.

Exactly how this supersaturation can be brought about is more difficult to see. Tributaries increase the population of the main stream, but they also increase the amount of food. The increase in space is a permanent addition, but the increase in dissolved food substances is merely temporary. After the plankton has used up the food added by the tributary, it will have to depend upon the resources of the main stream alone. Then the real competition begins. Supersaturation therefore is deferred for a time, but sooner or later, such a condition is bound to occur, with the consequent reduction in population.

Sometimes the decline which follows the peak reached by a tributary addition is in part the result of the elimination of certain tributary forms which could not stand the transfer to the new environment. On the other hand it is a common observation of biologists that when organisms are carried into a new environment they frequently find conditions so favorable that they increase beyond the limits set by the original environment. In economic entomology particularly there are many instances of organisms which barely maintained themselves in their native regions, but when these were unintentionally introduced into a new environment, they increased almost without restraint. With these facts in mind I consulted my data to discover similar instances among the plankton organisms with which I had been dealing, but no evidence of such an occurrence presented itself. The organisms peculiar to tributary waters invariably declined in numbers when introduced into the main stream.

The reason for this lack of conformity with the usual history of introduced organisms apparently lies in the wide dispersal and almost cosmopolitan character of the plankton. Spores and resting stages are carried far and wide by the wind. If a stream is suitable for a particular plankton organism which already exists in some neighboring pond or stream, then that stream cannot fail to be tested with respect to its suitability and the organism will develop there "spontaneously" so to speak. It may be postulated, therefore, that the indigenous plankton organisms of a stream are a chosen group selected by the environment from practically all species existing within the same region over which aerial dispersal is possible. Consequently a tributary form which could thrive in the main stream is already established there and such organisms as are peculiar to the tributary are organisms which are not adapted for survival in the main stream. If they were adaptable to conditions in the main stream,

they would in the past have become a part of the indigenous plankton assemblage there.

INFLUENCE OF THE TRIBUTARIES

It is natural that the tributaries should exert a marked influence on the plankton of the main stream, an influence proportionate to the amount of plankton which they carry and to the volume of water which they add, and dependent also upon the physical and chemical conditions of their waters. At times the plankton may be augmented in the river by contributions from the tributaries; again the percentage may be decreased by dilution following the introduction of barren storm waters from the side streams.

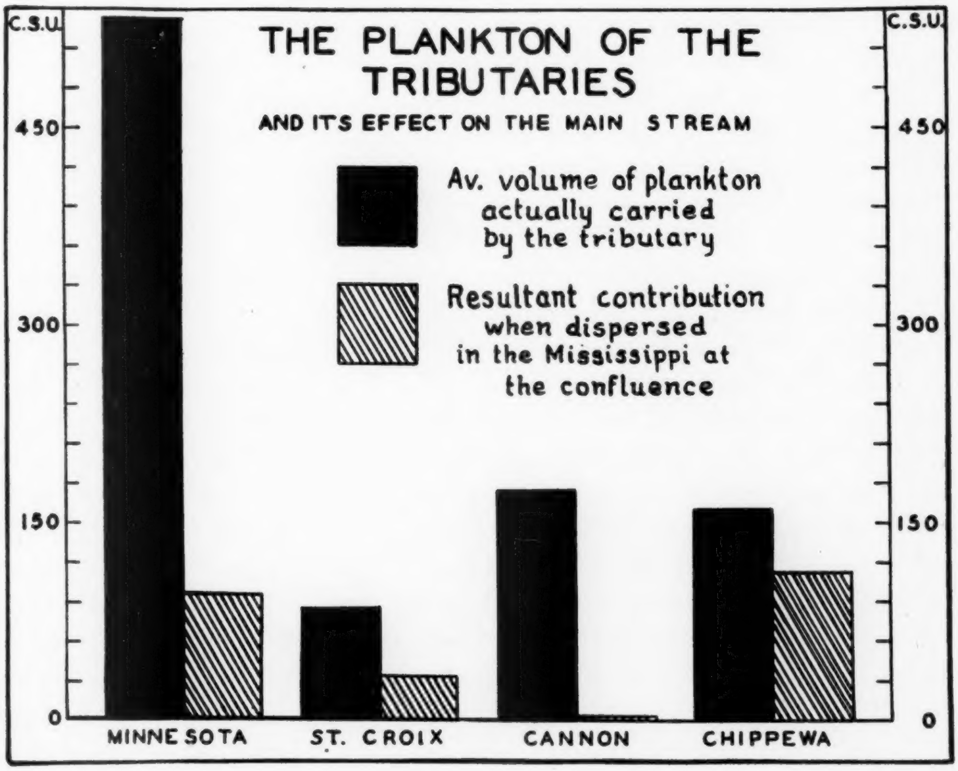


FIG. 7

The tributary itself may carry a great amount of plankton per unit of water, but when this plankton is added to the main stream the resultant contribution may be quite negligible because the total volume of water added is slight in comparison to the volume of water in the main stream. This is shown in Fig. 7 in which the calculations were based on the relative discharges and the consequent effect of dilution on the tributary plankton when this plankton was dispersed in the main stream. The Chippewa River, for example, carried an average volume of plankton amounting to 160 cubic standard units per cubic centimeter. But this plankton, when dispersed in the Mississippi at the confluence was diluted to 100 cubic standard units per

cubic centimeter since it was added to a stream whose combined volume of water now aggregated 1.6 times more than the tributary. The Cannon River added the least amount of plankton because of its slight discharge; the Chippewa River added the most.

The contributions of the tributaries are most noteworthy when they introduce into the plankton an organism different from any which the river carried previous to its union with the tributary. A case in point is the persistent presence of the diatom *Gyrosigma (Pleurosigma) spenceri* K. in the Mississippi below its junction with the Minnesota River. Galtsoff (1924) records *Gyrosigma spenceri* K. as being frequent in the plankton of the shallow water of Lake Pepin among the Potamogeton associations, but he does not place it among the diatoms of the river channel. Wiebe (1928) states that this species "is consistently much more abundant in the polluted sections of the river than in the tributaries" and concludes that *Gyrosigma spenceri* K. may be a tolerant species whose distribution possibly correlates with the degree of pollution. It will be noticed, however, if reference is made to Wiebe's tabular data, that this species does not appear in the Mississippi above the Minnesota River but it is present in the single collection from that tributary on August 17, and during September it occurs at Inver Grove and in diminishing amounts at the stations below as far down stream as Winona.

In Table No. X I have listed the occurrences of *Gyrosigma spenceri* K. for all stations included in the present survey. The numbers per liter of water have been averaged by months in order to compare the results with the monthly mean river discharge. During two months of the year this diatom occurred sparingly in the collections from Station No. 4, occasionally it appeared adventitiously in the plankton of the Cannon, Chippewa and St. Croix, but during most of the year it formed a conspicuous element of the Minnesota River plankton. The diminishing numbers recorded from the Mississippi River below the Minnesota River seem to indicate that the main stream receives its chief supply from the tributary but does not foster further development of this diatom in the channel plankton. It is significant to compare the survival of Gyrosigma with the strength of the current as indicated by the river discharge. During times of high discharge this organism is carried down stream as far as Winona. At other times it drops out somewhere in Lake Pepin. Since the transporting power of streams varies as the sixth power of their velocity, it follows that a slight change in velocity can produce marked differences in the ability of the stream to transport adventitious plankton organisms. This recalls the statement of Des Cilleuls (1926), who studied the phytoplankton of the river Loire, that Gyrosigma is a characteristic diatom of high water.

It is evident, therefore, that the Mississippi is seeded with Gyrosigma from the Minnesota River. But does the tributary itself produce this crop which is dispersed by the current or is it likewise seeded from another source?

TABLE X. *The Distribution of* Gyrosigma Spenceri K. *Compared with the Monthly Mean Discharge of the Mississippi at St. Paul. Wiebe's Records Are Similarly Tabulated Below For Comparison*

Month	Mean Discharge at St. Paul	Average Number of Individuals Per Liter											
		Sta. 1	Sta. 4	Sta. **5**†	Sta. 8	Sta. 9	Sta. **11**	Sta. **12**	Sta. 13	Sta. 15	Sta. **16**	Sta. 17	Sta. 19
Jan.	2,610	0	0	0	0	0	0	0	0	0	0	0	0
Feb.	5,060	0	0	17,000	7,000	3,500	0	0	1,250	0	0	0	0
Mar.	13,300	0	0	8,000	3,500	3,500	0	0	1,750	0	0	0	0
Apr.	17,500	0	0	9,500	1,500	2,000	0	0	650	250	5	120	250
May	11,300	0	0	5,000	0	1,100	0	0	1,000	100	750	40	10
June	5,780	0	0	6,500	300	1,100	0	0	10	0	0	0	0
July	6,470	0	0	26,000	3,800	2,800	0	0	380	0	0	0	0
Aug.	7,410	0	0	44,600	10,000	6,800	0	81	1,400	0	0	0	0
Sept.	10,500	0	1,000	75,000	10,000	7,000	10	93	2,250	15	0	22	0
Oct.	11,100	0	3,300	6,600	240	60	0	16	30	30	0	0	20
Nov.	7,390	0	0	375	225	160	0	12	20	0	0	0	0
Dec.	4,610	0	0	40	15	30	0	25	0	0	0	0	0
DATA FROM WIEBE, 1926													
Aug.	2,810	0	0	1,600	0	0	0	*	0	*	*	*	*
Sept.	8,630	0	0	*	16,045	16,150	0	*	2,030	*	890	*	800

* Indicates no collection.
† The tributary station numbers are printed in boldface type.

During the present year, 1930, I obtained a series of plankton samples from points on the Minnesota River far distant from the mouth. The collections were made during the first week in March. At the outlet of Bigstone Lake, which is the principal source of the Minnesota River, there was no trace of *Gyrosigma spenceri* K. in the plankton. Nor was this diatom present in the sample collected from the river below Ortonville and below the confluence of the Whetstone River, but at Granite Falls, 60 miles below Bigstone Lake, it was present to the number of 2,000 per liter, while at New Ulm it amounted to 12,000 per liter.

Between Ortonville and New Ulm the river flows through Marsh Lake and Lac qui Parle, which are both shallow and full of weeds. Many marshy stretches border the river in this upper section. This area then is probably the upper breeding ground for *G. spenceri* K., a diatom known to be developed in the littoral associations with water plants and filamentous algae and not an euplanktont. Doubtless the quiet weedy margins of the lower river also contribute a share.

TABLE XI. *The Influence of the Chippewa River on the Plankton of the Mississippi as Shown by a Selected List of Organisms*

Organisms	Average Number Per Liter			
	Outlet Lake Pepin	Chippewa River	Below Wabasha	Above Winona
Closterium moniliferum	3	40	10	8
Pandorina morum	190	565	435	430
Pediastrum duplex	890	1,500	1,490	1,030
Diatoma vulgare	140	6,330	3,550	3,330
Gomphonema acuminatum	0	1,700	225	860
Lysigonium varians	1,210	5,950	3,440	4,100
Navicula radiosa	0	930	470	570
Navicula sp.	620	8,330	2,330	2,280
Stephanodiscus niagarae	3,730	6,120	4,670	5,470
Synedra ulna	3,000	11,880	5,080	5,120
Ceratium hirundinella	4	310	170	20

While this discussion may appear to be of purely academic interest, it serves to bring out several significant points with regard to plankton and the biological applications of plankton study. It shows that a living organism may be passively carried by the current for many days and transported several hundred miles downstream, thanks to its remarkable survival potential. It is a confirmation of the opinion of most hydrologists (Kofoid, 1908) that the channel plankton of a river has in a large degree its source in the quiet backwaters of the river system. It further illustrates that in rheology certain characteristics of a plankton collection sometimes bear little relation to the immediate channel environment from which it was taken, a point that must be considered when applying the plankton method to stream pollution study through the use of the so-called indicator organisms. In another paper en-

titled "Notes on Aphanizomenon, with a description of a new North American species" I have discussed a similar seeding of the Mississippi River by a peculiar blue-green alga, *Aphanizomenon americanum* spec. nov., which also originates in the Minnesota River.

The influence of the Chippewa River is particularly noticeable on account of its great discharge and the close grouping of the sampling stations near the confluence of this tributary. In Table XI a selected list of organisms is given that best illustrates the plankton contribution of the Chippewa River to the Mississippi.

PART III

CONSTITUENT ORGANISMS OF THE PLANKTON AND THEIR SEASONAL DISTRIBUTION

CONSTITUENT GROUPS OF PLANKTON ORGANISMS

During the course of the year under consideration, approximately 190 species were identified from the channel plankton of the Mississippi River and its tributaries. These were distributed along the constituent groups as follows:

	Genera	Species
Phytoplankton:		
Myxophyceae	9	14
Rhodophyceae	1	1
Heterokonteae	2	2
Bacillariophyceae	26	60
Chlorophyceae	25	38
Total	63	115
Zooplankton:		
Mastigophora	7	10
Rhizopoda	4	4
Infusoria	18	18
Suctoria	1	1
Rotatoria	14	19
Cladocera	5	6
Copepoda	2	3
Miscellaneous	10	12
Total	61	73
Combined Total	124	188

A considerable portion of these species were undoubtedly tychoplanktonts but, since they were taken in the plankton, deserve consideration in virtue of their presence in the living state. Such temporary species affect the economy of the plankton sometimes as competitors, sometimes as adventitious food elements.

Tychoplanktonts are at times very numerous in the plankton. André (1926) made a special study of this question and concluded that it was the wind by means of the waves and currents which it provoked which played the principal rôle in the appearance of such adventitious forms in the plankton of the Rhone. He states moreover that these forms were able to remain in suspension in the water for a great number of days even after the disturbing force had abated, and my discussion of *Gyrosigma spenceri* K. has brought out the same fact.

AVERAGE PERCENTAGE COMPOSITION OF THE PLANKTON

In order to give some idea of the proportionate importance of the various major groups which go to make up the plankton, Table XII was constructed.

This table summarizes the data from all collections and gives the average percentage composition of the plankton on a volumetric basis. A volumetric system throws more light upon the ecological relations of the groups composing the plankton than does a system based on relative numbers since it reflects the relative quantity of living food material and the relative bulk of the plankton animals that utilize this food. The synthetic, or chlorophyll-bearing, organisms outmeasured in volume the analytic, or non-chlorophyll-bearing, organisms nearly 5 to 1.

TABLE XII. *The Average Percentage Composition of the Plankton on a Volumetric Basis*

	Cubic Standard Units per c.c.	Percentage of Total Plankton
Myxophyceae	13.6	6.3
Chlorophyceae	7.8	3.6
Bacillariophyceae	154.4	71.6
Green Flagellates	2.8	1.3
Total Synthetic	178.6	82.9
Colorless Protozoa	6.5	3.0
Rotatoria	13.4	6.2
Crustacea	17.0	7.9
Total Analytic	36.9	17.1
Total Plankton	215.5	100.0

In the Illinois River Kofoid (1903, 1908) found the same ratio of 5 to 1 when he compared the number of plant individuals with the number of animals. But this ratio increased to 18 to 1 when he included the green *Mastigophora* with the phytoplankton. Quantitative values are more significant than statistics in terms of individual organisms. The former takes into account size differences and estimates the amount of actual protoplasmic matter, be it in the form of a tiny Cyclotella or a massive Daphnia, which the system of individual counting would rank as equal. For each analytic unit of living plankton substance there were five units of living synthetic substance, and this result would seem to express in a general way the equilibrium of the biological components of the plankton of the Mississippi and its tributaries.

DOMINANT SPECIES

Shelford (1913) and his followers are accustomed to designate plant and animal communities by the names of the dominant organisms. Plankton from various localities and various environments can also be classified in this manner by assigning to the plankton (pelagic formation) of a particular lake or stream the name of the organism which predominated through the greatest period of time. What constitutes a dominant form appears to be a matter of opinion. The method of Pearsall (1929) regards as dominant all species

forming more than 66 per cent of the whole plankton, and as subdominant those which form more than 33 per cent of the plankton. I have used another system of classification, employing three categories: predominant, dominant, and subdominant. The ten most abundant species from each station were tabulated in descending order according to their relative abundance as given by the average for the year at that station. The organism having the highest average and ranking first in the list was called predominent (pd). Species ranking second to fifth in each group were regarded as dominant (d). The five remaining species, sixth to tenth in rank, were considered to be subdominant (sd). The results of this classification are given in Table XIII.

Somewhat similar results were obtained by another method of considering dominance. The most abundant species was selected from each of the 250 collections. These species formed the classes which were then seriated according to frequency. Thus, for instance, *Cyclotella meneghiniana* Bréb.

TABLE XIII. *Predominant (pd), Dominant (d) and Subdominant (sd) Plankton Species at the Various Stations*

Organisms	Mississippi River Stations								Tributary Stations			
	1	4	8	9	13	15	17	19	5	11	12	16
Cyclotella meneghiniana	pd	pd	pd	pd	pd	pd	pd	pd	pd	pd	pd	pd
Asterionella f. gracillima	d	d	d	d	d	d	d	d	d	d	d	d
Lysigonium granulata	sd	d	d	d	d	d	d	d	d	d	d	d
Synedra delicatissima	sd	d	d	d	d	d	d	d	d	sd	sd	sd
Synedra ulna	d	d	d	d	d	sd	sd	sd	sd	d	d	d
Scenedesmus quadricaudus	sd	sd	sd	sd	sd	sd	d	d	sd		sd	d
Aphanizomenon flos-aquae				sd	sd	d	sd	sd		d		
Diatoma vulgare	d	sd	sd								d	sd
Cocconeis placentula	d	sd									sd	
Gyrosigma spenceri			sd						d			
Stephanodiscus niagarae	sd	sd	sd	sd	sd	sd	sd	sd	sd	sd	sd	sd
Actinastrum han. fluviatile			sd	sd	sd	sd	sd		sd			sd
Lysigonium varians	sd	sd		sd				sd			sd	sd
Scenedesmus dimorphus					sd	sd	sd	sd	sd			
Pandorina morum										sd		
Fragilaria crotonensis										sd		
Fragilaria capucina										sd		

predominated the greatest number of collections, with *Lysigonium granulata* (Ehr.) Ralfs predominating the second greatest number, and *Asterionella formosa gracillima* Hantz. the third greatest. Again, the same method was applied to the predominating organisms on the basis of their volumetric or bulk importance instead of on the basis of individual numbers. Considered in this manner, it became noteworthy that only three or four species alternated in dominance through 70 to 80 per cent of the time. Nine species were predominant at times both on the basis of individual numbers and on the basis of volume. Eight species predominated only numerically and six species were predominant volumetrically without ever predominating through individual numbers. *Cyclotella meneghiniana* was the most abundant organism in 90

collections but was volumetrically the most prominent in only 48. *Lysigonium granulata* (including *L. crenulata*), on the other hand, predominated only 60 collections through force of numbers but was preëminent volumetrically in 114 collections.

This analysis was not applied to the zoöplankton principally because the methods adopted in this survey did not yield fair results with regard to animal types. One or two Cladocera might easily measure more in bulk than the entire nannoplankton content of the counting cell.

Another point brought out by these analyses was the shifting character of the plankton of young and swift streams as compared to the plankton stability of the impounded and older waters. The plankton of the Cannon and Chippewa Rivers is dominated now by one, now by another species which increases in numbers beyond all others. The quiet lakes adjacent to Stations 11 and 15 have the opposite effect. Here plankton dominance is restricted to a few species. Looked at in another way this difference is fundamentally the difference between the plankton of streams and of lakes. Streams possess a composite plankton with a great variety of constituent organisms, some indigenous, many others coming from tributary sources. Lakes in general produce a less varied supply and are not so strongly affected by conglomerated additions from other sources.

SEASONAL DISTRIBUTION

For the purpose of illustrating the seasonal distribution of the more important organisms of the plankton a diagram employing the spherical type of curve was constructed after the graphical method of Lohmann (1908). This manner of expressing results was also extensively used by Birge and Juday (1922) and these authors may be consulted for a discussion of the method of constructing such curves. Time is plotted along the abscissa and each vertical line represents a date of collection. The seasonal range of the organisms is represented by a horizontal band of varying width, which fluctuates in accordance with the number of individuals or colonies of a given species as they occurred in the collections from time to time. The width of the band actually represents the diameter of a sphere whose volume is numerically equivalent to the number of individuals per unit of water, in this case per liter. In other words, the numerical records for each species or group are represented by a series of spheres that are projected upon a two dimensional surface. It is important to note, therefore, that the width of the band is a function of the cube root of the actual number per liter. Hence a relatively slight increase in width is equivalent to a relatively marked increase in number of organisms represented.

The curves in Fig. 8 were made to represent the number of individuals or colonies of the various organisms per liter of water on a scale of $1 = 0.5$ mm. for phytoplankton and a scale of $1 = 1$ cm. for zoöplankton but the printed

figures are approximately one-fifth as large as the original diagram. One side of the graph is an average for the river above Lake Pepin and Inver Grove to Red Wing (Stations 8, 9 and 13); the other side averages the results secured from the river below Lake Pepin from Reads Landing to Winona (Stations 15, 17 and 19). These two stretches of the river are approximately of equal length and the number of collections for each group is the same.

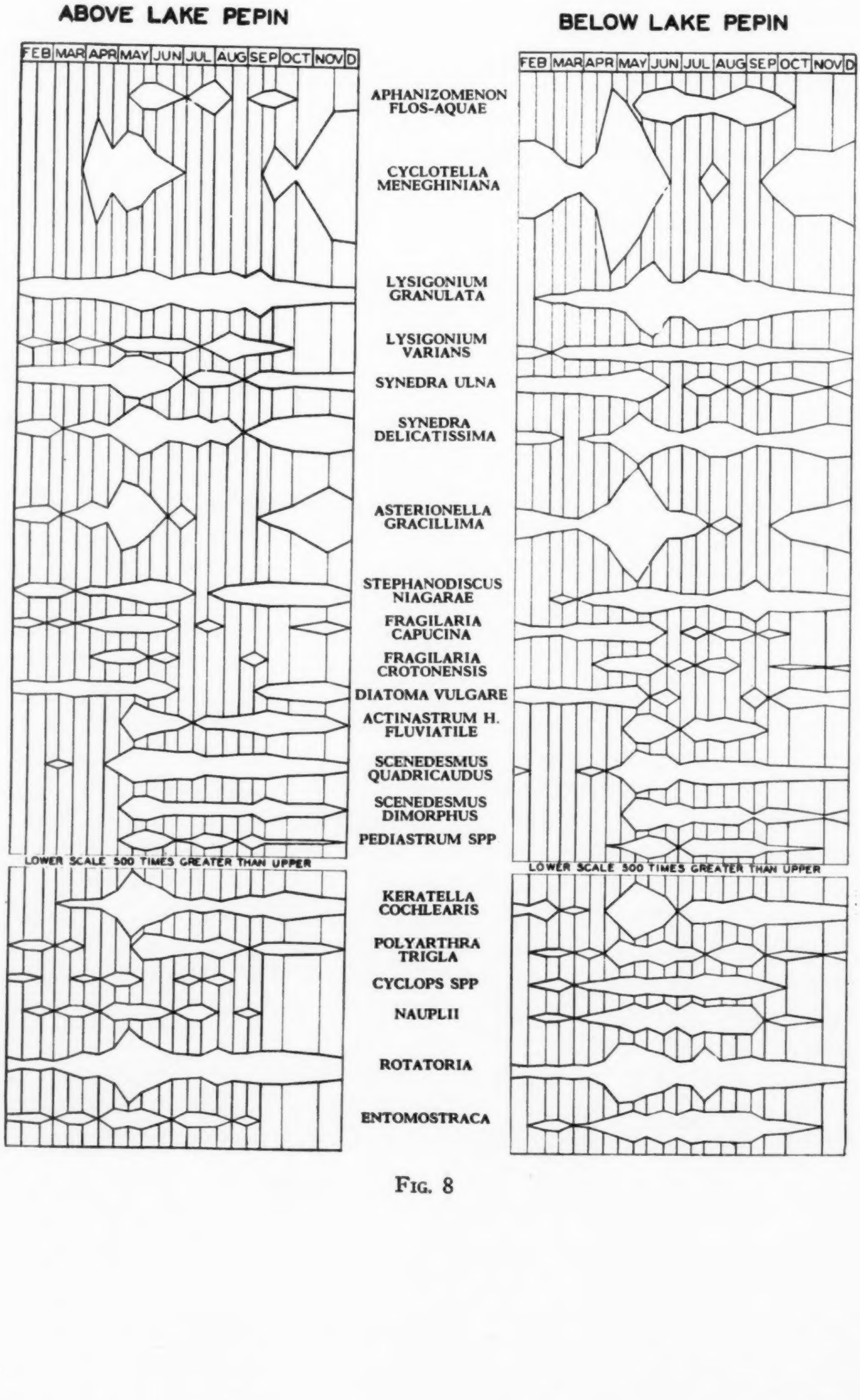


FIG. 8

Nevertheless there is a considerable difference in the corresponding curves, a difference which reflects numbers and seasonal distribution and gives some indication of the environmental differences between the upper and lower portions of the river.

DISCUSSION OF SPECIES

In the following pages the organisms occurring in the channel plankton of the Mississippi River and its tributaries will be taken up one by one and from the statistical data, resulting from the individual and volumetric counts, facts will be cited pertaining to the relative abundance of these organisms, their seasonal distribution and autecology wherever the data warrants such conclusions.

MYXOPHYCEAE

The *Myxophyceae* with the exception of *Oscillatoria chlorina* Kuetz. were prevalent at high temperatures and were favored by hydrographic stability. The greatest numbers appeared during the warm weather period from the end of May to the end of September. The sharp rise during the early summer was succeeded by a sudden decline in the first part of July due to severe flood conditions especially in the tributaries. By end of July the Blue-green Algae had recovered from this set-back and rose again to a peak, then dwindled at a slow rate and were wiped out again by the unstable water conditions and lower temperatures of October and November.

At the mouth of the Minnesota River and at the outlet of Lake Pepin the *Myxophyceae* were more abundant than at other stations. Here they were favored by a semi-limnetic environment.

The representation of *Myxophyceae* in the plankton during 1928 was not as strong as it should have been. This was in part due to abnormal high river levels during the year. The numbers actually present were also minimized by the centrifuge. Nevertheless a total of 14 species were identified from the collections and were distributed as follows:

Anabaena flos-aquae Bréb. This species was of frequent occurrence during June, July, and August, but was usually not numerous in individuals. The maximum, 28,000 per liter, appeared in the Minnesota River on June 20.

Anabaena affinis Lemm. was recorded once or twice from the Mississippi River.

Aphanizomenon americanum spec. nov., discussed fully in another paper (1931) by the author, formed a water bloom in the Minnesota River on July 31.

Aphanizomenon flos-aquae Bréb. Observed at all stations excepting Camden. It was present in every collection at Stations 15, 17, and 19 from the end of May to the end of September and was most abundant below Lake Pepin. In the field it was often seen in the water at the time when samples were being collected and sometimes formed a distinct bloom in the Cannon

River, but when these samples were examined microscopically after centrifuging, the Aphanizomenon appeared to be relatively scarce. Notwithstanding the heavy losses, this species contributed the greater share to the volumetric pulses of the *Myxophyceae*. It appears to require stable water conditions and high temperatures for its optimum development.

Aphanocapsa sp. Rare in the river during the spring and summer. Reported by Wiebe (1928) in small numbers.

Coelosphaerium Naegelianum Ung. Only seven or eight scattered entries of a few colonies occurring in August and the winter months found a place in the records.

Gloeocapsa sp. Recorded once in September at Winona. May have been overlooked in other collections since Wiebe reports it more frequently in 1926.

Lyngbya sp. This genus was of rather common occurrence in 1926 according to Wiebe, but it appeared in the 1928 collections only four or five times in very small numbers.

Merismopedia sp. Fairly common in the river from the end of May to the end of September. Less frequent in the tributaries. Occasional colonies noted in the other months of the year. Maximum, 8,000 per liter in Lake Pepin on August 15.

Microcystis aeruginosa Kuetz. Occurred sparingly in July, August and September. Recorded mainly from Camden, Reads Landing, and Winona.

Oscillatoria chlorina Kuetz. was present only at the beginning of the survey when the rivers were covered with ice. It disappeared in March with the break-up of the ice and the advent of flood waters. The number of filaments fluctuated between 1000 and 4000 per liter during the first three series of collections, then became scarce and disappeared entirely by the end of March. It was rather uniformly distributed through the entire river and occurred also in the tributaries. This species was so persistent in the plankton when the river was frozen over and was so widely distributed that it may be considered a facultative plankton alga, thriving equally well under littoral or open water conditions.

Oscillatoria limosa Ag. was encountered sporadically throughout the year in small numbers. It was present in six collections from the Cannon River and at other stations where the current was swift. Moreover, it was found principally during high water stages, which appears to indicate that it is an adventitious addition to the plankton torn loose from the bottom by the current.

Oscillatoria princeps Vauch. This large species, clearly a waif in the plankton, appeared sparingly in eight collections. It was localized in the Mississippi River between the Twin Cities and Red Wing.

Oscillatoria tenuis Ag. like the preceding was found principally in the

river above Lake Pepin. It occurred irregularly from July to November but never in any considerable quantity.

RHODOPHYCEAE

The red algae are in almost all cases marine plants. Chantransia is one of the very few exceptions. It occurs in fresh water and according to J. E. Tilden "it is rare, being usually discovered in very cold fresh water, such as rapidly flowing streams, and in shaded spots, under cliffs, under bridges, or under water mosses which provide protection from the light." An undetermined species of Chantransia was encountered in the plankton at Camden on July 6 and again on July 16. Only a few broken plants were seen.

HETEROKONTEAE

Botryococcus Brauni Kuetz. occurred rarely in the collections. A few colonies (25 per liter) were recorded on June 20 at the outlet of Lake Pepin.

Tribonema minus (Wille) Hazen. This species was of irregular occurrence in the plankton and was never abundant.

BACILLARIOPHYCEAE

The diatoms were at all times the most important constituents of the plankton from a volumetric viewpoint. Considering volume as expressed by cubic standard units, the diatoms provided 75 per cent of the average total plankton of the Mississippi River. In the tributary waters diatoms were likewise predominant, making up 64 per cent of the total mass of plankton in the Minnesota River, 59 per cent in the St. Croix, 77 per cent in the Cannon and 85 per cent in the Chippewa River. Combining all collections from all stations, the average was 72 per cent.

The earliest spring peak in diatom production came on March 25 at the outlet of Lake Pepin and was due almost entirely to Cyclotella. Excluding this unique case, the principal vernal pulse of the entire group occurred on May 9 at Camden and at the Lock and Dam, on May 23 in the river between the Twin Cities and Lake Pepin, and on June 6 in the river below the lake. The June pulses in the lower river far exceeded any of the May records for the upper river. The tributaries varied between the same dates: May 9, Cannon River; May 23, St. Croix and Chippewa Rivers; June 6, Minnesota River. The order of occurrence of the vernal pulses seems to bear some relation to the relative age of the water. The late pulses are generally the greatest and appear to profit by accumulating the harvest from the upper stretches of the river.

With the exception of the Minnesota River no station exhibited a real increase over the vernal diatom pulse throughout the rest of the year. In this tributary there were a series of recurrent cycles, the amplitude of which constantly increased and finally culminated in December with an immense amount

of Cyclotella. Starting with 400 cubic standard units of diatoms on June 6, the diatom curve for the Minnesota River dropped to 75 a month later, then increased to 604 during the middle of August, two weeks later dwindled to 115, rose to 982 at the end of September, decreased to 182 in October, increased again in November to 560 and terminated in a grand climax of 2143 on December 13.

The list giving the composition of the plankton of the Mississippi River and of Lakes Pepin, Keokuk and St. Croix as found by Galtsoff (1924) included only nine species of diatoms. Dr. Albert Mann examined some of Galtsoff's collections from different parts of the river and came to the following conclusions with regard to the diatoms:

> "It is noteworthy that the range of species in all the gatherings is small as compared to the usual fresh-water diatom flora; also that they have a close resemblance to each other, although their geographical range is considerable. It is interesting to find that several almost cosmopolitan fresh-water forms are absent; for example *Navicula (Stauroneis) phoenicenteron, N. major,* such Surirellae as *S. biseriata* (E.) Breb., *S. splendida* (E.) K., *S. cardinalis* Kitt., and the almost universal *Melosira varians* Ag., unless the *M. subflexilis* K., sparingly found in Lake Keokuk, can be taken as a variety of that species. On the other hand, *Melosira crenulata* and its too close relative, *M. granulata,* are very abundant in nearly all samples. Neither of these species is at all frequent east of the Mississippi but appear from the river westward, and the latter of the two, *M. granulata,* formed vast beds of new fossil diatoms extending over the northwest part of the United States and running into Canada around Deadmans River, British Columbia."

In the course of the present survey particular attention was paid to the diatoms of the plankton. Approximately 60 species were identified and these included five of the six species named as absent by Dr. Mann. The most abundant species are about twelve in number. A discussion of the various species, arranged in alphabetical order, follows:

Amphora ovalis Kuetz. was occasionally found in the Mississippi principally during spring floods. More common at Camden than elsewhere. Numbers, few.

Asterionella formosa gracillima Hantz. This was one of the principal components of the river plankton and one of the most striking and orderly in its seasonal distribution. The vernal pulse came during May at all stations excepting the Chippewa River, where the vernal maximum was delayed until the first week in June. Following this there was a rapid decline in numbers and the organism practically disappeared during midsummer. In September it began to rise again, reaching its autumnal peak during November above Lake Pepin and during December below Lake Pepin. At Winona this organism reached a maximum of 1,840,000 frustules per liter on May 23 and at this station likewise it enjoyed the greatest prevalence as shown by an average of 141,500 per collection. The greater abundance at the lower stations may

be looked upon as a cumulative effect although there does appear to be evidence that this species is unfavorably affected by pollution. Dividing frustules were noticed at Camden on April 25 and May 9 at temperatures of 6-8°C. Below Lake Pepin this condition did not appear until May 22-June 5 at temperatures of 18-20°C. Temperature alone does not offer an adequate explanation of the definite pulses and no correlation could be worked out between temperatures and the times when the maxima occurred at the various stations.

Campylodiscus hibernicus Ehrbg. This unusual diatom was recorded from Camden, Inver Grove, Reads Landing and Wabasha. Very rare.

Cocconeis pediculus Ehrbg. This diatom occurred somewhat irregularly in the collections throughout the year. The maximum, 32,000 per liter occurred on June 6 at Camden where it was more prevalent than at other stations. It was also abundant in the Cannon River.

Cocconeis placentula Ehrbg. was twice as abundant as the preceding species. It was perennial in the plankton but most frequent in the spring and fall. It appeared at Camden during every month of the year and gave indications of a spring pulse (36,000 per liter) on June 6 and an autumnal pulse (69,000 per liter) on September 24. The species of Cocconeis are usually noted as epiphytic upon algae but the detached frustules were numerous enough in the channel collections to merit the opinion that they are also truly planktonic as well as sessile.

Cyclotella meneghiniana Bréb. This diatom, minute in size, made up for its smallness by extremely great numbers and so contributed largely to the volumetric records. It reached tremendous importance in the spring and fall but declined to minimum numbers in midsummer and midwinter. The spring maxima did not occur simultaneously at all stations. On April 11 the maximum appeared at Inver Grove and Hastings; on April 25 at the Lock and Dam, St. Croix, Lake Pepin outlet, Wabasha and Winona; on May 9 at Camden, the Cannon River and Red Wing; on May 23 in the Minnesota and Chippewa rivers. It was present most consistently at the outlet of Lake Pepin where the spring run culminated in 10,000,000 per liter. The fall peak also varied in appearance between October and December, but at eight of the twelve stations the autumnal maximum came in the collection of December 13. In general the spring peaks were preëminent but the reverse occurred in the Minnesota River and as a consequence this tributary so increased the numbers of Cyclotella at Inver Grove, Hastings and Red Wing that the December entries at these stations exceeded the spring records. The December collection from the Minnesota River was so dense with Cyclotella that the enumeration ran to 21,000,000 per liter. A species so abundant as Cyclotella cannot fail to play an important part in the ecology of the plankton and collections made with the silk net, through which this diatom readily escapes,

would give no adequate picture of the plankton at the time when Cyclotella was prevalent.

Cymbella affinis Kuetz. This very small diatom was not uncommon at Stations 1 and 4 during February and March and again during June. It was also recorded from the Chippewa River in February and appeared in small numbers at a few other stations. *Cymbella cymbiformis* (Kuetz.) Bréb., *C. ehrenbergii* Kuetz., *C. gastroides* Kuetz., *C. lanceolata* Ehrbg., *C. prostrata* Berk., and *C. tumida* Bréb. were also recorded sparingly from various stations during the early part of the year.

Cystopleura (Epithemia) turgida Kuetz. occurred sparingly in the Mississippi and the Minnesota Rivers mostly during the winter months and at flood time. *C. turgida* var. *granulata* (Ehr.) Grun. was found once on February 1 in the Chippewa River and *Cystopleura (Epithemia) sorex* Kuetz. was of rare occurrence in the Mississippi.

Diatoma vulgare Bory. The important rôle played by Tabellaria in lake plankton and by *Fragilaria virescens* Ralfs in other rivers appears to be taken over by *Diatoma vulgare* in the upper Mississippi. Kofoid (1908) considered this an adventitious species in the plankton of the Illinois where it occurred sparingly at irregular intervals, and Allen (1920) noted it only three times in the San Joaquin River. In the Mississippi survey of 1928 it was one of the most common constituents of the plankton and was reported at all stations with entries for every month of the year. It was most numerous at Camden, next in magnitude in the Cannon River, and also prevalent in the Chippewa River. Lake Pepin, Lake St. Croix, and the Minnesota River carried the least amounts. It occurred therefore most commonly in the swifter streams and was least abundant in the quiet lake-like waters. This species had a seasonal distribution similar in all respects to that of a typical plankton organism. There were at least two pulses at each station, one in May or June, the other in October or November. At Camden there was evidence of a pre-vernal pulse on March 26 in addition to the pulses on June 6 and November 19. The river above Lake Pepin derived its principal supply from Camden and Cannon River. In Lake Pepin this organism dropped out, making only a single appearance at the outlet in October during high water. The stations below Lake Pepin were in turn seeded with *Diatoma vulgare* from Chippewa River.

This organism is reputed to have a mesosaprobic character. At first glance the present data appears to contradict this for Diatoma decreases from Stations 1 to 9. This decrease may be attributed in part to the pool above the Twin City Lock and Dam which acts as a settling-basin. It seems more logical therefore to intepret the relative prevalence of the species in accordance with the hydrographic conditions rather than with pollution.

Eunotia sp. was very uncommon in the Mississippi and the Minnesota rivers.

Fragilaria capucina Desmaz. was reported in every month of the year and noted at all stations. A strong vernal pulse occurred during May but there was not definite autumnal pulse. (It had precisely the same seasonal distribution in the San Joaquin River according to Allen.) The spring peak came somewhat later and rose to higher proportions below Lake Pepin. Chains of frustules were counted and these aggregations, variable in the number of cells, reached a maximum of 16,000 per liter on June 6 at Winona. The maximum above Lake Pepin was 8,000 in May. It was abundant in all the tributaries except the Minnesota River where it occurred only during May and June but where it produced the greatest volumetric record of 75 cubic standard units per cubic centimeter.

Fragilaria crotonensis (Edw.) Kitt. was not as abundant as the preceding species and was confined principally to the spring months. It appeared in the Mississippi at the end of April, reached its greatest abundance at the end of May and the beginning of June, then dwindled away. From September to December it was present again but in scattered and small occurrences. It was more common in the Wisconsin tributaries and at Winona than elsewhere. The ribbon-like chains of this species were always composed of fewer frustules than the long bands of *F. capucina*.

Fragilaria mutabilis (W. Sm.) Gun. occurred sparingly in the spring months below Lake Pepin.

Frustulia rhomboides Ehr. was listed two or three times from the Mississippi at Camden. Rare.

Gomphonema acuminatum Ehr. was fairly common except during midsummer. Present in all but the July collections from Camden. Maximum 24,000 per liter. It always occurred as isolated frustules, having apparently been detached from the pedicels during the process of centrifuging.

Gomphonema constrictum Ehr., *Gomphonema gracile* Ehr., and *Gomphonema sphaerophorum* Ehr. were also identified from the plankton material but were so uncommon that they did not appear in the counts.

Gyrosigma scalproides Rabenh. was recorded sparingly from August to November below Lake Pepin, in the lake outlet and in the Chippewa River.

Gyrosigma spenceri W. Sm. This species, derived from the waters of the Minnesota River, has already been fully discussed in an earlier part of this paper in connection with the influence of the tributaries on the plankton of the main stream. Maximum record, 90,000 per liter on September 24. Average for the Minnesota River, 20,153 per collection.

Lysigonium (Melosira) granulata (Ehr.) Ralfs. Identification unsatisfactory and includes *L. crenulata* (Ehr.) Kuetz. These closely related species could not be separated under the low power which had to be employed while counting. The long filaments of these diatoms were frequently the most conspicuous organisms in the plankton. In certain collections they outnumbered in individuals and outmeasured in bulk all other constituent plants and

animals of the sample. Since it is believed that *L. granulata* was much more abundant than its too close relative, the discussion will be given under that heading.

This diatom was listed in practically every collection from each station, thus taking rank as the generally most frequent plankton of the Mississippi River. A well defined vernal pulse occurred May 23 at most stations. This was anticipated in the Cannon River by two weeks and delayed a fortnight in the Minnesota River and below Lake Pepin. The delayed vernal pulse at Wabasha and Winona appeared to be a cumulative effect running to 452,000 and 556,000 filaments per liter which was greatly in excess of the records at the stations above. At intervals from then on secondary pulses were noted at many stations and the organism periodically fluctuated in numbers until the close of the year. The interval between minor pulses was about one month. It was one of the very few organisms which showed increases during the midsummer plankton minimum. Auxospore formation was noticed on August 1.

This organism was most abundant in the Minnesota River, averaging 72,743 per collection, about three times more abundant below Lake Pepin than above the lake and least common at Camden.

Lysigonium (Melosira) spiralis Kuetz. was noted during July and August but was included under *L. granulata* in the totals since it appears to be but a variety of that form.

Lysigonium (Melosira) varians Ag. This common species of somewhat irregular occurrence was recorded in all months of the year. Its seasonal distribution can best be traced in the Chippewa River where it was most numerous. There it occurred in every collection, reached a maximum of 16,000 per liter on June 20, declined somewhat through July and August, increased again to 12,000 per liter on September 12 and dwindled through the winter. Its occurrence below Lake Pepin was strongly influenced by this tributary. Above the lake it also exhibited spring and fall maxima but of lesser magnitude. This common and almost cosmopolitan species was rare in the St. Croix River and strangely absent from the Minnesota River.

Meridion circulare (Grev.) Ag. appeared on May 9 in the Chippewa River and again at Wabasha. It seems to be adventitious.

Navicula spp. Considerable effort was expended in the beginning to classify the various forms of Navicula and to keep separate counts of each. But the species were so numerous and the differences mostly so imperceptible under the lower magnifications which were required while counting that the statistical results appeared to be open to much questioning. The species listed below were carefully determined from the plankton material, but only general statements concerning them are reliable. The distribution of the group as a whole may merit mention. Large numbers of Navicula were at all times a characteristic of the Cannon River which is a swift and shallow

stream. Undoubtedly the largest portion were adventitious, but the average per collection in this tributary runs to over 72,000 per liter. The largest single entry was 437,500 per liter on October 15. The Chippewa River and the Mississippi at Camden were also consistently rich in Navicula, but the averages there fall far short of the great density reported for the Cannon River. Lake Pepin at the outlet had very few of these diatoms. It would appear that current velocity and depth are the principal factors concerned in the local distribution. There is certainly no correlation between the numbers of Navicula and the degree of pollution.

Navicula affinis Ehr. *(Neidium affine)* and *N. oblonga* Kuetz. were rare in the Minnesota River.

Navicula americana Ehr. was recorded from the Mississippi above Lake Pepin on two occasions, small numbers of *N. dicephala* (Ehr.) W. Sm. appeared in the Mississippi during the early part of the year, and *N. radiosa* Kuetz. was fairly common at all the stations.

Navicula rhyncocephala Kuetz. was one of the most common members of the genus in the river above Lake Pepin and also common in the Cannon River.

Navicula viridula Kuetz. was very common in the Cannon River during the last three months of the year. On October 15 it amounted to 94,500 per liter at this station. *N. gracilis* Kuetz. was also very common there in the early collections.

Nitzschia (Homoeocladia) sigmoidea (Nitzsch) W. Sm. This large species is apparently adventitious in the plankton. It was placed on record five times at Camden, twice at Red Wing and once each at Inver Grove, Wabasha and Winona. In the Cannon River it appeared in six collections. The numbers were always very small.

Nitzschia (Homoeocladia) spp. Under this heading are included three or more species of Nitzschia all of which were identified with uncertainty, viz. *Nitzschia sigma* W. Sm., *N. linearis* (Ag.) W. Sm., and *N. palea* (Ehr.) W. Sm. These were never abundant and the occurrences were scattered. The entries show a decided concentration in June and July with about 4000 per liter in the maximum records and erratic occurrences in other months of the year. This may corroborate Allen's observation (1920) that Nitzschia is favored by high temperatures.

Pinnularia major (Kuetz.) W. Sm. was satisfactorily identified once from the St. Croix River, and *Pinnularia socialis* Palmer was doubtfully determined from the Mississippi at Camden.

Rhoicosphenia curvata (Kuetz.) Grun. appeared three times in the Cannon River, once in the Chippewa River and once or twice in the Mississippi. Recorded in February, May, June and September. Fairly common on May 10 in the Cannon River.

Rhopolodia gibba (Kuetz.) Muel. appeared once in the Mississippi above the Twin City Lock and Dam during June.

Sphinctocystis (Cymatopleura) elliptica W. Sm. Nine records of small occurrences during winter and spring. Observed in the plankton of the Mississippi, Minnesota and Cannon rivers. Maximum 40 per liter.

Sphinctocystis (Cymatopleura) solea (Bréb.) W. Sm. was often present in the first three months of the year with scattered records of small numbers throughout the rest of the year. It did not appear in the first and second collections after the break-up of the ice. The occurrence of this species and of other adventitious diatoms mainly under the ice cover is probably due to the greater scouring action of the confined waters upon the river bed at this time of the year.

Stauroneis phoenicenteron Ehr. was frequent in the Mississippi between the Twin Cities and Red Wing, but occurred in small numbers. Heavier representation in first half of year. Also noticed in the Cannon River from May to August. Probably favored by sewage pollution.

Stephanodiscus niagarae Ehr., an important plankton in Mississippi River water, occurred in all months of the year and at all stations. The Minnesota River carried the largest amounts as shown by an average of 10,529 per collection. The Cannon River was a close second with 7,382 per collection and the Chippewa River ranked third with 6,119 per collection. The preëminence of this centric diatom in these tributaries may be correlated with the presence of great limnetic environments in the drainage basins of these streams, for Stephanodiscus is more at home in limnetic waters than it is in a lotic environment. The principal breeding grounds of this diatom are the lakes and quiet back-waters. This fact and hydrographic conditions may account for the somewhat erratic pulses which pervaded the river plankton. Thus on May 9 this species appeared at the mouth of the Cannon River in such numbers as to establish a record for the year, 80,000 per liter, preceded by 16,000 on April 25 and followed by 28,000 on May 23. Since these were the months of maximum stream flow, it appears that the high waters transported this diatom from the upper lakes to the mouth of the stream. In the Minnesota River the vernal pulse came late, on June 20, at a time of low water when the river itself assumed the quiet character of a lake. In the Mississippi River the vernal maxima came during May and June. The autumnal pulses occurred during September and October. The midsummer minimum was restricted to July.

Surirella biseriata (Ehr.) Bréb. was recorded four times during February and March in small numbers. It appeared in the Minnesota River and at Inver Grove and Red Wing. The latter stations apparently received this organisms from the tributary above.

Surirella ovalis Bréb. was present in the Mississippi from Inver Grove to Winona. It was common in the Minnesota River, rare in the Cannon River

and not recorded for the St. Croix or Chippewa rivers. This diatom appeared in March and was most prevalent during April, May and June. It was not seen during July and August, but appeared again sparingly from September to November. The maximum record was 8,000 per liter on May 9 at the time of the vernal pulse.

Surirella splendida W. Sm. was one of the rarest diatoms in the collections. Only two specimens were seen. It was found in the Chippewa River and in the outlet of Lake Pepin.

Synedra delicatissima W. Sm. This needle-like diatom is an important constituent of the river plankton. It was common at all stations and was recorded throughout the year. The earliest pulse came on May 9 at Camden and at the Lock and Dam. The vernal pulse was retarded in the Cannon River until June 6. At all other stations there was a strikingly large and uniform pulse on May 23, which reached record proportions (293,000 per liter) in the Minnesota River. This species persisted in diminished numbers throughout the summer and rose again in October and November to a moderately high autumnal peak.

Synedra ulna Ehr. was most abundant during the first six months of the year but was evidently perennial and certainly not strictly adventitious. This species had a large vernal pulse in May at all stations, was common during June, less frequent in July and August, with feeble pulses during the autumn. It was one of the principal diatoms at Camden where it averaged 33,048 per collection and reached a maximum of 136,000 per liter on May 9. The records give no evidence that it is favored by pollution.

Tabellaria flocculosa (Roth.) Kuetz. The genus Tabellaria which abounds in the plankton of lakes in many parts of the world and is at home in Lake Superior and some of the northern Minnesota lakes was not found at all in the Mississippi River. *Tabellaria flocculosa* occurred only in the Chippewa River during April, May and June, showing a maximum of 16,000 per liter on June 6.

CHLOROPHYCEAE AND *CONJUGATAE*

The *Chlorophyceae* were well represented both in species and individuals but the dominant forms were of such a small size that volumetrically this assemblage appears to be of minor importance compared with the other algae. The leading genera in order of their importance were Scenedesmus, Actinastrum, and Pediastrum.

As a group the *Chlorophyceae* increased rapidly during May when they were swept into their greatest prominence by a strong vernal pulse. The midsummer decline was not as pronounced as in the other groups of plankton organisms. Recurrent pulses during the summer months kept the volume of green algae well sustained until September when the numbers began to wane and gradually fade to insignificant proportions during the winter. The species

encountered in the plankton are discussed in alphabetical sequence and the *Conjugatae* are here included with the *Chlorophyceae*.

Actinastrum hantschii fluviatile Schröd. This variety is distinguished from the typical form by its pointed cells. It was common throughout the summer and fall and appeared at all stations, exhibiting the greatest prevalence in the Minnesota River. During May it made its first appearance and persisted thenceforth in the plankton until December. The strongest pulses came in May and in September. This variety does not seem to be mentioned in the plankton literature of this country. The typical form *Actinastrum hantschii* Lagerh. was not seen at all in the Mississippi plankton and it is probable that the records of Galtsoff and Wiebe refer to the variety *fluviatile* described by Schröder.

Chlorella sp. An undetermined species was noticed at times in the plankton, but due to its small size it was omitted in the enumeration.

Closterium acerosum Ehr. was found in about fifteen collections scattered through the summer and fall months. The greatest abundance was 60 per liter.

Closterium gracile var. *elongatum* W. & G. S. West, while never conspicuously abundant, was often in the plankton especially during the fall months. It was found at all stations excepting Camden, the Cannon and the Chippewa. The greatest number, 6,000 per liter, occurred at Hastings on July 16.

Closterium Kuetzingii Bréb. was recorded once from the Chippewa River on November 19 and *C. turgidum* Ehr. appeared in the St. Croix on the same date.

Closterium moniliferum Ehr. was the most conspicuous of the desmids by reason of its large size and frequency in the collections. It was present at all stations, occurring irregularly from March to October, and was especially frequent in the Chippewa River. The most numerous occurrence came in May and June. The greatest number found was 200 per liter.

Closterium striolatum Ehr. appeared sporadically in three or four collections, never exceeding 25 per liter.

Coelastrum microporum Naeg. occurred sparingly from August to November with a maximum of 12,000 per liter at Winona on September 12. There are seventeen records for this species. The greatest number of coenobia were encountered in August and September. *C. sphaericum* Naeg. was recorded twice at Camden.

Cosmarium spp. Occurred sparingly from June to October. More abundant in the Chippewa River than elsewhere.

Crucigenia quadrata Morren. Scattered records during June, July and August. Not found in the tributaries. Most abundant at the outlet of Lake Pepin where it reached a maximum of 10,000 per liter on June 20.

Dictyosphaerium pulchellum Wood. During August and September col-

onies of this species occurred in the plankton at Hastings and at stations below. The greatest number observed was at Wabasha, 7,000 per liter, on August 30. This genus was reported by Wiebe in small numbers during the same months of 1926.

Eudorina elegans Ehr. is mainly a spring form in the Mississippi River. It appeared at the end of March, reached its peak during April and tapered off during May. There are scattered records of its occurrence during the summer and fall with indications of a slight pulse during the middle of August. The maximum catch occurred at Hastings on April 11 where colonies of Eudorina numbered 860 per liter. This species was somewhat more abundant in the polluted sections of the river although it is commonly considered to be a clean-water form. Galtsoff (1924) found it to be of scarce occurrence in Lake Pepin and above the lake during August and September. Wiebe (1928) reported it from various stations in the Upper Mississippi and his records show a greater abundance in August than in September.

Gleocystis sp. Recorded once at Inver Grove, March 26, 20 per liter.

Hydrodictyon reticulatum (L. Lag.) was noted only twice and in very small amounts at Red Wing and at Wabasha.

Micractinium pusillum Fres. was observed once on May 23 in the Minnesota River.

Oocystis sp. occurred sparingly during August. The greatest abundance recorded was 2,500 per liter on August 17 at Hastings. Wiebe (1928) noted this genus once during September at St. Paul.

Pandorina morum Bory. This colonial flagellate was more abundant than its close relative *Eudorina elegans* Ehr. It reached a maximum of 27,500 per liter in the St. Croix River on June 6. The largest records came during June and the beginning of August. Throughout the rest of the year the records are small and scattered. It appeared at all stations but was most abundant in the Wisconsin tributaries and the lower river between Red Wing and Winona.

Pediastrum duplex Meyen. The principal occurrences of this species were centered in the late spring and early fall. It was the most abundant member of the genus, less common at the heavily polluted stations than in the cleaner areas.

Pediastrum boryanum (Turp.) Menegh. had somewhat the same seasonal distribution as the preceding species but lacked the autumnal pulse. It was recorded from only 29 collections while *P. duplex* was present in 59 collections. Both species appear to be absent from the Minnesota River.

Pediastrum integrum Naeg. was recorded once at Hastings on June 21 (20 per liter). According to Smith (1920) it is a chance wanderer in the plankton from the littoral region.

Pediastrum simplex Rab. occurred in only four collections, on June 21 at Hastings, 20 per liter; on August 1 and 15 at Reads Landing, averaging 3,000 per liter; on September 24 in the Minnesota River in very slight amounts.

Quadrigula lacustris (Chod.) Smith was of rare occurrence in the Wisconsin tributaries. It was also present in the September collection from Lake Pepin to the extent of 30 per liter.

Scenedesmus abundans var. *brevicauda* Smith was seen once at Camden on February 29, and *S. arcuatus* Lemm. occurred sparingly from May until the close of September.

Scenedesmus bijuga (Turp.) Lag. was noted in August and September in that portion of the river between Red Wing and Winona. It did not exceed 4,000 per liter in any collection.

Scenedesmus dimorphus (Turp.) Kuetz. appears to be confined to the warmer parts of the year. It had a well defined vernal pulse on May 23 and June 6, and a lesser autumnal pulse in September. Though only about half as abundant as the following species it formed a conspicuous part of the phytoplankton during the summer.

Scenedesmus quadricaudus (Turp.) Bréb. was perennial in the plankton. The major pulse came at the end of May and lesser pulses followed at intervals during the warm months. From November to April this species persisted in reduced numbers. The largest number, 104,000 per liter, was recorded in Lake Pepin on May 23. It was by far the commonest of the *Chlorophyceae*. Although sewage water is favorable for the development of this species the numbers recorded from the Mississippi stations do not correlate with the degree of pollution.

Spirogyra spp. Fragments of Spirogyra, principally *S. porticalis* (Müll.) Cleve, were found occasionally in the summer and fall collections at all stations excepting Camden and the Minnesota River. They appeared most frequently at Inver Grove, Hastings, and Red Wing.

Staurastrum paradoxum Meyen. This desmid was found in the plankton during October in very small amounts. The maximum number was only 30 per liter. It is principally a limnetic species and its appearance in October coincides with high water levels.

Stigeoclonium lubricum (Dill.) Kuetz. This adventitious alga appeared occasionally at Reads Landing, Wabasha and Winona.

Tetraspora sp. Apparently of little importance in the plankton. Recorded once during June at Red Wing. Wiebe (1928) also records it but once.

Fragments of the filamentous algae Ulothrix, Mougeotia, and Zygnema, and such attached forms as Chaetophora and Cladophora appeared occasionally in the channel plankton as drift from the benthic zone.

MASTIGOPHORA

The flagellates as a group were poorly represented in the plankton of the Mississippi River. The average volume of the year of the flagellate population of the Minnesota River was twelve times greater than that of the Mississippi.

The year 1928 was a period of relatively high water as compared to previous years, and this may account for the sparse occurrence of *Mastigophora* in the river channel. In the Minnesota River the greatest abundance came in the warmest months, June, July, and August, when this tributary was at a low level. The predominant pulse, 96,000 per liter, coincided with the striking water bloom of *Aphanizomenon americanum* spec. nov. on July 31. Another unusual occurrence of Mastigophora was observed in the plankton of the St. Croix River on June 6. Green flagellates, chiefly Cryptomonas and Chlamydomonas, numbered 130,000 per liter and were associated with the largest single catch of Pandorina (27,500 per liter). Representatives of the chlorophyll-bearing flagellates, excluding Pandorina and Eudorina, which have already been considered in connection with the *Chlorophyceae,* will now be briefly discussed.

Ceratium hirundinella O. F. M. was practically absent above Lake Pepin. Insignificant numbers were present once in the Minnesota River, twice in the St. Croix River and twice in the outlet of Lake Pepin. In the Chippewa River however, this organism appeared to be thoroughly at home from June to October. Two pulses were noted, one of 4,000 per liter on June 20 and another of 1,500 per liter on September 24. Since the influence of the Chippewa is strikingly reflected in the plankton of the Mississippi at the stations below the confluence of this tributary, it is not surprising that Ceratium was taken at Wabasha and Winona, and there exhibited the same seasonal range and pulses as in the tributary but with numbers much smaller and occurrences less frequent. Though a common plankton in other waters, this organism is apparently unable to thrive in the sewage-laden courses of the upper Mississippi. The Chippewa was unique in having a good representation of Ceratium. In this stream the average number per liter collection was 324.

Cryptomonas ovata Ehr. was confined principally to the St. Croix River where it was most abundant in the June collections.

Euglena: Various species of Euglena were determined from time to time including *E. acus* Ehr., *E. ehrenbergii* Kuetz., *E. spirogyra* Ehr., and *E. viridis* Ehr. but the counts were not kept apart. The maximum abundance was 16,000 per liter on July 6 in the Minnesota River. This genus occurred principally from May to October.

Glenodinium gymnodinium Penard. This dinoflagellate was reported mainly in July with a maximum of 4,000 per liter in the Minnesota River. The Minnesota and the Chippewa rivers appeared to be the sources of supply for the small numbers which were occasionally observed in the Mississippi.

Phacus longicaudus Ehr. occurred sparingly in the plankton principally during the summer months.

RHIZOPODA

Only a few rhizopods were noticed in the plankton fauna. These were numerically of no importance and were predominantly of an adventitious

character. Galtsoff (1924) listed three genera, Arcella, Centropyxis, and Difflugia from the upper Mississippi and these were recorded as very scarce. His list comprises five named species, *A. vulgaris* Ehr., *C. aculeata* St., *D. pyriformis* P., *D. corona* W. and *D. lebes* P. The latter species was reported only from Lake Keokuk. In 1928 I detected only the following forms:

Arcella vulgaris Ehr. This form was found in the plankton less than a dozen times. Most of the occurrences, small numbers in each case, came in the river above Lake Pepin and accompanied flood conditions.

Centropyxis aculeata Stein was even less common than Arcella. Isolated individuals appeared in only three samples.

Difflugia sp., a bottom organism, was occasionally encountered in the Mississippi plankton.

Euglypha sp. This bog-loving rhizopod appeared in the plankton of the Chippewa River on August 1.

INFUSORIA

The planktonic ciliates of the Mississippi are a badly neglected group, yet they above all others appear to furnish the best criteria for the biological analysis of water in respect to pollution and the progress of recovery. But their specific determination is fraught with so many difficulties, particularly when only preserved material is available for study, and their small size makes confident counting so unreasonably arduous that the plankton investigator generally pays little heed to this class of organisms. Thus Galtsoff (1924) mentioned only two species of Infusoria, and Wiebe (1928) omitted the entire group.

The samples collected during 1928 contained a variety of ciliates, an account of which was taken for the volumetric estimates, but the determinations, except of the large and conspicuous forms, were generally very sketchy. About twenty species were recognized from time to time including the following:

Codonella cratera (Leidy) (*C. lacustris* Entz.) does not play a very significant part in the plankton of the Mississippi, although it was recorded in every month of the year and appeared at one time or another at all stations. The maximum numbers were recorded in May for all stations except the Minnesota River where it occurred only in July and August. Feeble autumnal pulses were noticed in September and October. In the Cannon River the greatest concentration was observed, 8,000 per liter, on May 9. This organism is often used as an indicator of polluted conditions but the data collected during 1928 offers no evidence to substantiate this view. It was more abundant in the clean waters of the St. Croix than at any point along the heavily contaminated Mississippi.

Colpoda sp. This ciliate was common in the more grossly polluted section of the river during the season of ice coverage. The maximum was about 4,000 per liter.

Halteria grandinella O. F. M. occurred irregularly in the plankton collections but at times was quite common especially above Lake Pepin and in the Minnesota River.

Paramecium sp. Small numbers were taken in the plankton at Inver Grove and Hastings during June and August. Maximum, 75 per liter.

Stentor sp. This protozoan was recognized but twice, once in the St. Croix River and once at Reads Landing. It may have been *Stentor coeruleus* Ehr. since that is the species recorded for Lake Pepin by Galtsoff (1924).

Tintinnidium fluviatile St. appeared in the spring plankton of the Mississippi River in fairly large quantities but was not recognized at the time so that no reliable figures are at hand to describe its occurrence.

Vorticella spp. Isolated individuals and small clusters were seen in the plankton in every month of the year. Every station has contributed a share to the records, but a slight preponderance is credited to Red Wing and the least number to Camden. The colonial Vorticellidae, Carchesium and Epistylis, also appeared at irregular intervals during the summer, mostly at Inver Grove and Hastings.

Various other forms of ciliated protozoa were encountered but the nature of the preserved material made accurate identification impracticable. Some were partially identified and referred to the following genera: Bursaria, Colpidium, Condylostoma, Euplotes, Frontónia, Loxophyllum, Nassula, Strombidium, and Stylonichia.

SUCTORIA

Acineta was the only form recognized in the plankton. The records show but four occurrences and these were single unattached individuals. This form occurred at Camden, Reads Landing and Wabasha.

ROTATORIA

The predominant volumetric pulse of rotifers occurred at the end of May coincident with the volumetric maximum of total plankton organisms. The average volume of rotifers for the Minnesota River was almost four times greater than the greatest average volume of any other station. This high average for the tributary was not due to a few collections only but was the result of a continuous abundance of rotifers throughout most of the year. Approximately 20 species were recorded from the Mississippi and its tributary waters during 1928, and a number of others were left undetermined. Galtsoff (1924) found 34 species and Wiebe (1928) recorded 8 genera.

Asplanchna sp. occurred sporadically in the collections from May to November. It was found in the Minnesota and Mississippi Rivers. Maximum, 25 per liter. *Asplanchna amorpha* Hud. was the common form recorded by Galtsoff.

Brachionus patulus O. F. M. (*Noteus militaris* Ehr.) was found in small

numbers at Reads Landing and Wabasha. Scarce in Lake Pepin according to Galtsoff.

Brachionus spp. Under this heading are included *B. angularis* Gos., *B. pala* Ehr., *B. bakeri* O. F. M., and perhaps several other forms. The last two named were the most common members of the genus. Brachionus was found throughout the year and was listed for each station except the Cannon River. The Minnesota River provided two-thirds of the total number recorded. A maximum of 810 individuals per liter was observed there on May 23. There was a well developed vernal pulse followed by a midsummer minimum with weak autumnal pulses in August and September. The average for the Minnesota River, all collections, was 84 per liter. Galtsoff (1924) reported a dozen forms of Brachionus from the upper Mississippi.

Diurella stylata Ehr. was found sparingly during the summer and fall and was likewise recorded by Galtsoff as scarce.

Euchlanis dilatata Ehr. During August and September a few specimens were taken at the outlet of Lake Pepin and at Wabasha. Galtsoff lists this species as scarce in Lake Pepin and did not note it at any of the river stations.

Filinia (Triarthra) longiseta (Ehr.) Recorded from May to September with greatest abundance in June and July. Most common in the Minnesota River where it reached a maximum of 525 per liter on June 6. Infrequent in the St. Croix and Cannon rivers and not found in the Chippewa. Rare below Lake Pepin but fairly common in the river above the lake due undoubtedly to the influence of the Minnesota.

Keratella (Anuraea) cochlearis (Gosse) was the most abundant rotifer in the plankton, was found at all stations, and was recorded during every month of the year. It exhibited a strong vernal pulse during May and a lesser autumnal pulse during October. Very common in the Minnesota River, averaging 518 per liter, and establishing a maximum record there of 2,825 per liter on May 23. Next in abundance at the outlet of Lake Pepin, and least common in the Mississippi at Camden. This species and the variety *tecta* were reported by Galtsoff.

Keratella quadrata O. F. M. (*Anuraea aculeata* Ehr.) This spring form appeared in the Mississippi River during April and May. In the Chippewa River it was confined to the April collections but in the Minnesota River its appearance was delayed to May 23 after which it was taken again on June 6. The maximum record was 110 per liter on May 9 at Reads Landing. Lake Pepin also furnished the largest average number of individuals. This rotifer was more common in the Minnesota and Cannon rivers than at any other station excepting No. 15 in the lake. At all stations it disappeared in June and was not seen again throughout the remainder of the year.

Lecane (Cathypna) luna O. F. M. Found once in the Chippewa River during August. Recorded by Galtsoff only for Lake Keokuk.

Notholca striata O. F. M. occurred sparingly in Lake Pepin and below the

lake during the spring months. Also found in the Chippewa River. Not listed by Galtsoff.

Pedalia mira (Huds.) A solitary individual was observed in the plankton of the Mississippi on August 17 at Red Wing. This species was recorded by Galtsoff only for Lake Keokuk.

Polyarthra trigla Ehr. (*P. platyptera* Ehr.) a perennial rotifer, was second in abundance to *Keratella cochlearis* and had the same local distribution as that species. It was likewise most common in the Minnesota River, averaging 78 per liter, with a maximum in that tributary of 560 per liter on July 6. The pulses were of irregular occurrence and gave indications of recurrent cycles from May to October. Less frequent at Camden than in the river below. Also infrequent in the Chippewa and Cannon rivers. Recorded as scarce by Galtsoff.

Rotifer spp. Wiebe (1928) found the genus Rotifer abundant in the polluted section of the Mississippi and employed it as an index organism. My study of this group was too inadequate to enable me to draw conclusions from my data, but this genus was undoubtedly common in 1928 although most of the occurrences are probably listed among the unknowns.

Synchaeta stylata Wierz. During the fall of the year this species was recorded once from the Minnesota River and once from Lake Pepin. Galtsoff found it to be frequent in Lake Pepin.

Testudinella (Pterodina) patina (Hermann) was recorded once from the Chippewa River during May.

Trichocerca spp. Several species of *Trichocerca (Rattulus)* doubtfully referred to *T. cylindrica* (Imhof) and *T. longiseta* (Schrank) occurred sporadically in the collections principally during August and September. Galtsoff listed three species of *Rattulus* from Lake Pepin, viz. *Rattulus rattus* M., *R. pusillus* L. and *R. stylatus* G.

In addition to the species already named above, Galtsoff (1924) listed the following rotifers from the upper Mississippi: *Notops brachionus spinosus* R., *Monostyla cornuta* O. F. M., *Monostyla lunaris* E., *Monostyla bulla* G., *Schizocerca diversicornis* v. D. and *Anuraeopsis hypelasma* G.

ENTOMOSTRACA

The Cladocera and Copepoda were the only crustaceans of any importance in the plankton, but their showing in the records is unsatisfactory for various reasons. The manner of collecting the sample and the small amount of water centrifuged, while adequate for securing nannoplankton, are not very suitable methods for the study of the larger zooplanktonts. Even though present in small numbers in the concentrated material the crustaceans may fail to reach the small counting cell. Despite such difficulties the counts were made as accurately as possible by endeavoring to secure a representative amount of the concentrate and by counting the number throughout the entire cell.

Crustaceans were much more prominent below Lake Pepin than above the lake and this is to be expected since the lake offers a habitat more suitable for them than does the river. Galtsoff (1924) found that the water flowing into Lake Pepin carried about 8,000 copepods in each cubic meter while the water at the outlet of the lake carried from 44,000 to 46,000 per cubic meter. This same investigator made an extensive qualitative and quantitative study of the crustaceans in Lake Pepin and in the upper Mississippi. He listed nine species of Cladocera for Lake Pepin, six species for the river above Lake Pepin, and four species for Lake St. Croix. He did not separate the Copepoda into species but recorded them as a group. Wiebe (1928), working in the same territory during 1926 found Cyclops, Diaptomus, Simocephalus, Bosmina, Moina, Daphnia, Chydorus and Ceriodaphnia.

CLADOCERA

Six species of Cladocera were identified in the collections. Although few in numbers the large bulk of the individuals added considerably to the volumetric records.

Bosmina longirostris O. F. M. The only records for this species are as follows:

May 23	Cannon River	158	per liter
" 23	Winona	40	"
June 6	Lock and Dam	20	"
" 6	Minnesota River	175	"
" 6	Inver Grove	20	"
" 6	Hastings	25	"
" 6	Red Wing	20	"
Aug. 29	Wabasha	20	"
Sept. 12	Wabasha	20	"

Chydorus sphaericus O. F. M. was recorded but once, on May 9 at Wabasha, 10 per liter.

Daphnia pulex (De Geer) occurred once in the Cannon River, 40 per liter, on May 9.

Daphnia longispina O. F. M. One occurrence at Reads Landing, 10 per liter on May 23, and on the same date 40 per liter at Winona.

Leptodora kindtii Lill. Fragments of this crustacean were noticed during July and September in samples from the outlet of Lake Pepin. This large organism is evidently broken up by the centrifuge.

Moina rectirostris (Leydig). One record for the Minnesota River, July 16, 120 per liter.

COPEPODA

Since the Copepoda were represented only by a few species no discussion of the whole group appears necessary. Notes on the various species are given below.

Diaptomus oregonensis Lill. occurred only in the plankton of the St. Croix River and in the Mississippi below Lake Pepin. Five records during July and September. Maximum, 35 per liter, at Wabasha.

Cyclops spp. Several species of Cyclops were represented in the plankton. These species included *Cyclops bicuspidatus* Claus and *Cyclops viridis* Jur., but the former apparently furnished the principal numbers. The Minnesota River, the outlet of Lake Pepin, and the river at Wabasha each contributed about one-fourth of the total numbers; all other stations combined produced the remaining 25 per cent. Cyclops was recorded from 61 collections scattered through the year, but the majority were reported from May to September. The maxima never exceeded 190 per liter. The average per collection for all stations was only 9 per liter.

Nauplii: These larval copepods showed practically the same characteristics of seasonal distribution and of distribution among the various stations as did the preceding group. In individuals however they outnumbered Cyclops more than two to one. They appeared in 80 collections, were most numerous at Wabasha, and next in abundance at Reads Landing. Winona and the Minnesota River were also largely responsible for the average of 22 per liter for all collections.

MISCELLANEOUS INVERTEBRATES

Nematoda: Unstable hydrographic conditions which result in the movement of bottom sediments often bring nematodes into the plankton. These worms are adventitious and temporary inhabitants among the floating population of the waters. They occurred in 41 of the 250 collections and generally but one or two appeared in the counting cell. No attempt was made to determine the species. It was significant however that the number of occurrences at the various stations was somewhat proportional to the amount of sewage pollution. Thus at Camden nematodes were present in only one collection, at the Lock and Dam in two collections, at Inver Grove in nine, at Hastings in eight, at Red Wing in four, at Reads Landing in two, and at Wabasha and Winona in one collection respectively. Since these worms thrive in the midst of decaying organic matter and bottom sludges, this distribution curve is not purely accidental and results in part from the character of the bottom deposits in the various sections of the river.

Oligochaeta: Stylaria, Chaetogaster and Nais were noticed on rare occasions in the plankton.

Tardigrada: Macrobiotus was found only once, at Reads Landing during May.

Hexapoda: Rare and isolated occurrences of Ephemerid nymphs, *Croixidae*, and chironomid larvae were noticed, but these had no significance in the general plankton ecology.

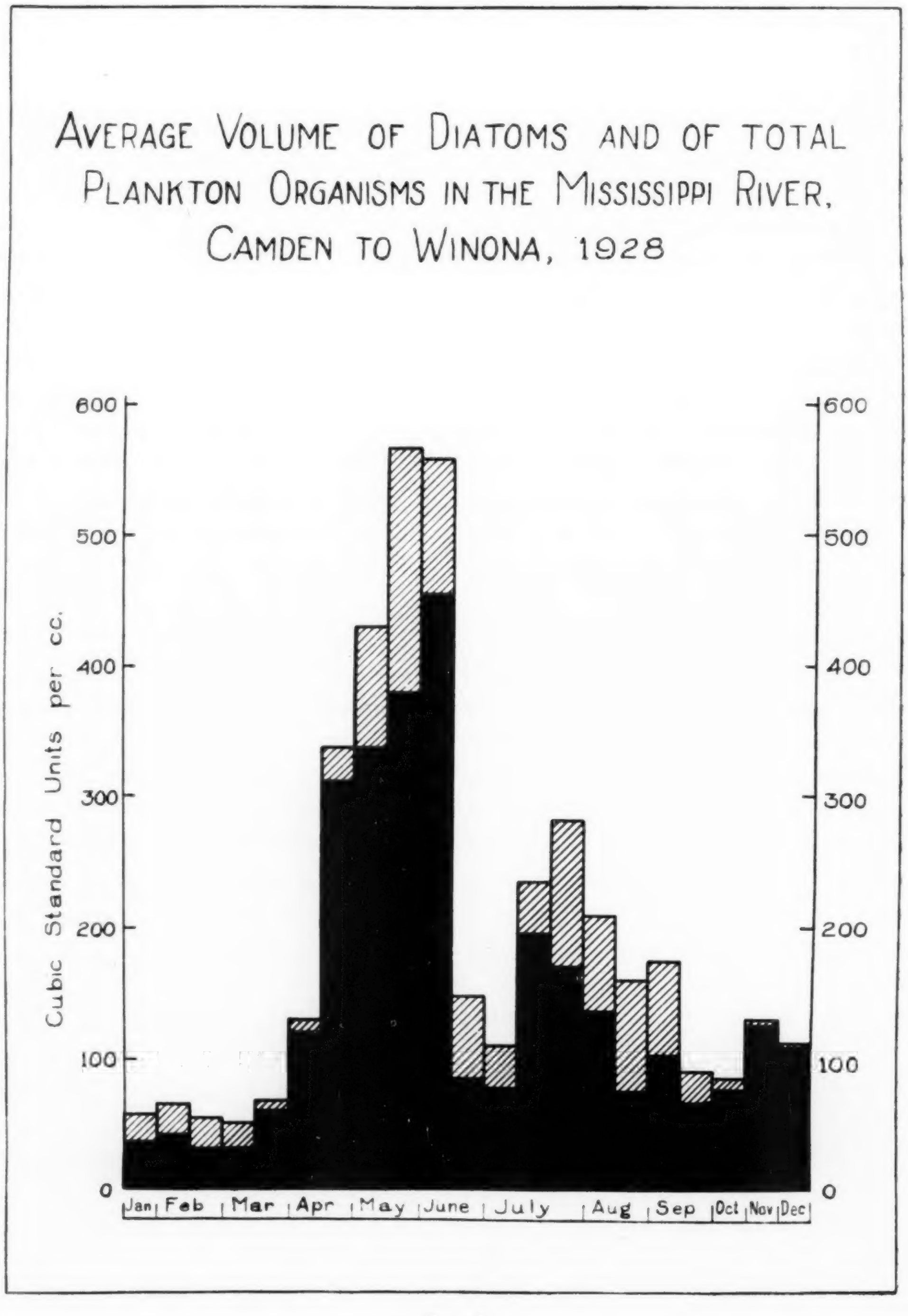

AVERAGE VOLUME OF DIATOMS AND OF TOTAL PLANKTON ORGANISMS IN THE MISSISSIPPI RIVER, CAMDEN TO WINONA, 1928
Cubic Standard Units per cc.
600
500
400
300
200
100
0
Jan
Feb
Mar
Apr
May
June
July
Aug
Sep
Oct
Nov
Dec

FIG. 9

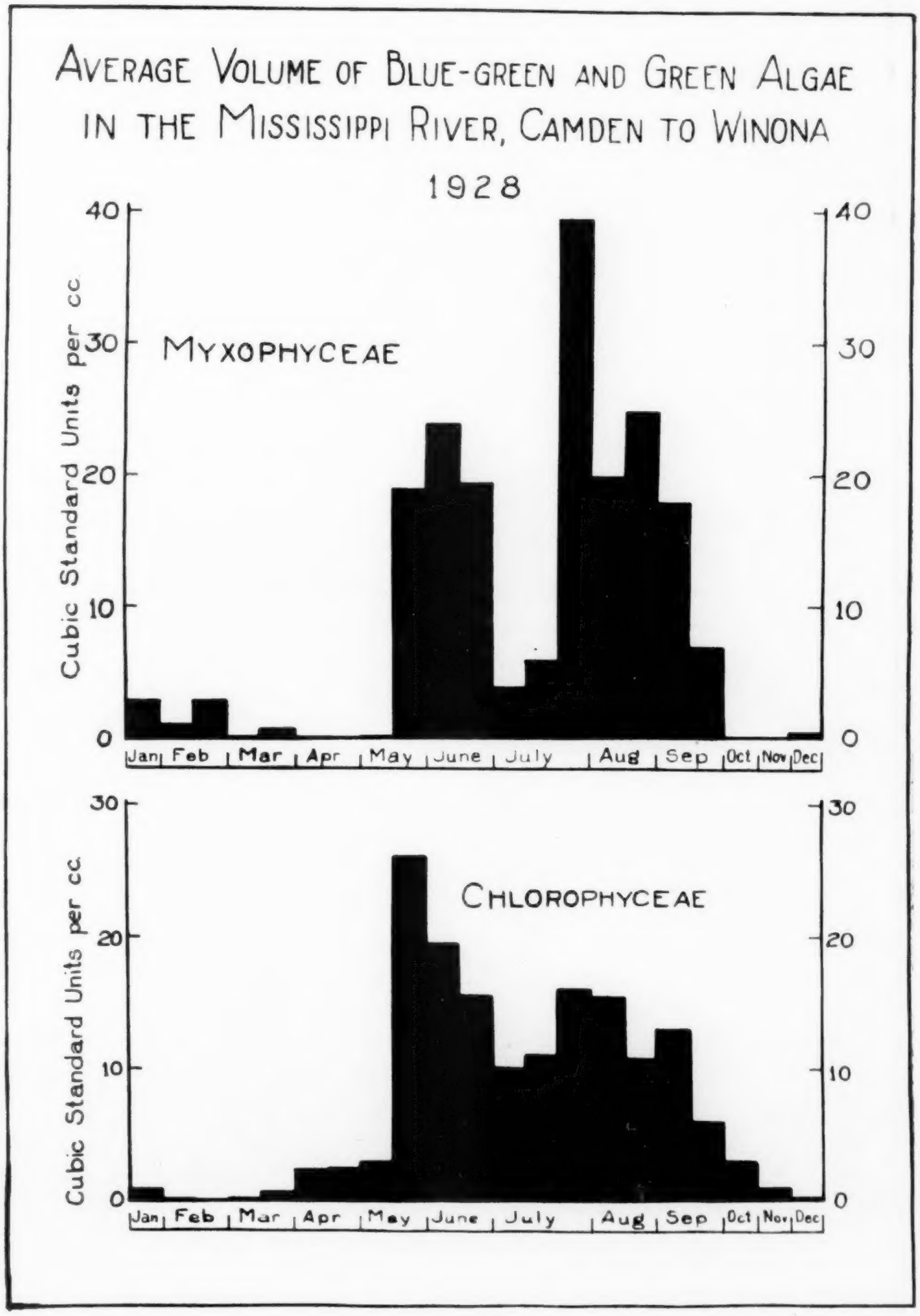

AVERAGE VOLUME OF BLUE-GREEN AND GREEN ALGAE
IN THE MISSISSIPPI RIVER, CAMDEN TO WINONA
1928
MYXOPHYCEAE
CHLOROPHYCEAE
Cubic Standard Units per cc.
Cubic Standard Units per cc.
0
10
20
30
40
Jan
Feb
Mar
Apr
May
June
July
Aug
Sep
Oct
Nov
Dec

FIG. 10

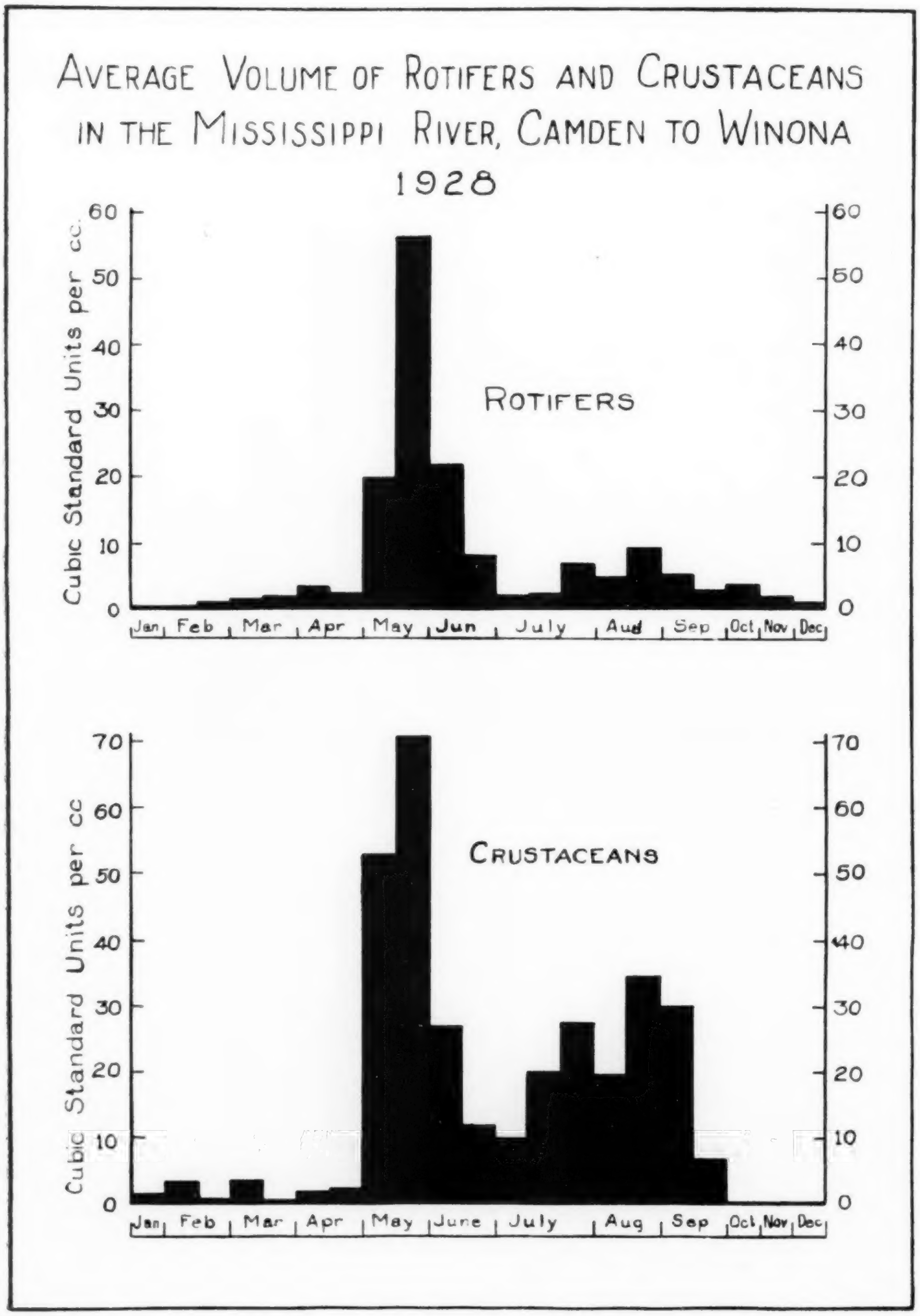

AVERAGE VOLUME OF ROTIFERS AND CRUSTACEANS
IN THE MISSISSIPPI RIVER, CAMDEN TO WINONA
1928
Cubic Standard Units per cc.
ROTIFERS
0
10
20
30
40
50
60
Jan
Feb
Mar
Apr
May
Jun
July
Aug
Sep
Oct
Nov
Dec
Cubic Standard Units per cc
CRUSTACEANS
0
10
20
30
40
50
60
70
Jan
Feb
Mar
Apr
May
June
July
Aug
Sep
Oct
Nov
Dec

FIG. 11

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THE VEGETATION AND HABITAT FACTORS OF THE COARSER SANDS OF THE NORTH CAROLINA COASTAL PLAIN:

AN ECOLOGICAL STUDY

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THE VEGETATION AND HABITAT FACTORS OF THE COARSER SANDS OF THE NORTH CAROLINA COASTAL PLAIN: AN ECOLOGICAL STUDY

Introduction

To one who travels in the coastal plain of the Southeastern United States, one of the most distinctive vegetation-habitat complexes is that of the erect, tenuous-bladed wire grass *(Aristida stricta)* in scattered tussocks on the dry loose sand hills and ridges. If trees are present they will in the most xeric areas be the long leaf pine *(Pinus palustris)* and the turkey oak *(Quercus Catesbaei)*. On more favorable sites, black jack oak *(Q. Marylandica)*, blue jack oak *(Q. brevifolia)*, or the scrub post oak *(Q. Margaretta)* will be present. A soil characteristic will also help identify these areas for the casual observer: That is the more or less prominent patches or even large areas of pure white coarse sand, which upon examination is seen to form a thin mantle or surface layer over a darker humus-bearing layer beneath. On pioneer areas where the wire grass is absent and little or no humus has as yet appeared in the soil, the uniform brilliant white of the rain-washed quartz sand is suggestive, particularly at night, of snow covered ground. A walk over these white low ridges, constituting the bare areas or pioneer stages of these coarser sands, during a clear midday in July or August will remind one far more of a hot desert than anything else; the almost total reflection of the sun's heat and light will so enhance the ordinary downward radiation as to make an excursion over such areas very uncomfortable indeed. As the vegetation cover comes in, this effect is progressively minimized.

In the responses of both the herbaceous and woody plants, the dry character of the habitat is also evinced. The water content of these plants is relatively low and thus subjects all such areas to perennial fire danger; the wire grass will burn anytime of year after one day of clear weather following rain. "Sandhill country," for so such areas are commonly designated, is a huge tinder box.

As a matter of more than casual interest, attention should be called to the fact that it is in this soil habitat of North Carolina that the long leaf pine, freed from competition by factors to be discussed later, reached its greatest development (Ashe, 1). No other pine can establish itself in the more xeric areas and only one broad-leaved tree, the turkey oak, can enter, but unlike the pine, being sensitive to fire, it can offer little competition.

An anonymous contributor to a survey of the counties in 1810, writes from Moore County, a county of the well known "Sandhill District," in the south central region of the State. "The sandhills yield no other tim-

ber than yellow pine [an old name for long-leaf] which from the sameness and uniformity of appearance, affords too little variety to be pleasing to the view. The gentle inequalities of the surface are all that relieves the wearied eye."

It may be easily shown that the well known original distribution of the virgin loblolly forests chiefly in the northern half of the North Carolina coastal plain and the long leaf in the southern half has a basis in the distribution of soil types. Now that the long leaf pine is gone the principal crops grown on the loose sands of its typical habitat are cotton, tobacco, peaches, dewberries, corn, and small grains.

This paper deals with the native vegetation and soil factors controlling this, with some practical applications of the information gained. The plant communities and their successional relations extending from the pioneers on the white sands to the closed communities merging into the mesic oak-hickory forest, will be discussed. The soil habitat analysis will cover the most significant soil factors, that of the water relation being the most important. This intensive ecological study of the "sandhill" vegetation, a habitat of the southern coastal plain, is the first to be made. The authors too well realize the complexities of the problem in relation to the limited resources available in their attack upon it. Nevertheless, we believe our data have enabled us to make a beginning, at least, in the matter of properly evaluating the primary and indirect habitat factors which have set apart these very distinctive communities. We desire to express our appreciation of the field work done by Mr. A. C. Martin, formerly Assistant Professor of Botany, State College, who carried on some studies on the sandhill vegetation. He added many plants to our lists and made some field tests before the present authors turned their attention to the problem.

THE VEGETATION

In the study of plant distributions on the coarser sands, the early stages of the succession will be emphasized. These predominate because of frequent fires and are of exceptional interest because of the very distinctive vegetation which represent them.

In the earlier lists of plants of the southern coarser sands the species have been given with little or no regard to their water relations. In this account for the first time, the herbaceous as well as woody plants have been classified into the five clearly distinguishable communities as these are found to be dependent upon the controlling water factor. These are, as already indicated, extreme xeric, the xeric, xero-mesic, mesic, and hydric phases of Quercus-Aristida communities. Aristida does not appear in the first or pioneer stage but is present and generally dominant in the succeeding four phases.

These four phases, as will be shown later, are respectively the xeric-

Aristida consocies (developmental community with a single dominant) of the Quercus-Aristida associes, the xero-mesic Aristida-Quercus (Marylandica) mictium (mixture of two vegetations belonging to different stages of succession), the mesic Aristida-Hicoria mictium and the hydric Aristida consocies of the Campulosus-Panicum bog associes (major developmental community). Of especial interest is the fact that *Aristida stricta* together with *Pinus palustris* may play a dominant rôle in two associes.

It must be made clear at this point that the present native communities of plants throughout the coastal plain represent plant aggregations surviving under frequent fires. So frequent and so certain everywhere is fire that the Aristida communities represent what might well be called "fire subclimaxes," stabilized communities which are prevented from normal successional changes by the destructive action of the pyric agent. The probable succession or sere which would take place without fire will be discussed later under the heading "The Sere."

In the matter of organization of the communities the system of Clements (3) will be followed and in plant nomenclature the standard Manual of Southern Plants by Small (10), will be adhered to.

QUERCUS-ARISTIDA ASSOCIES: PIONEER STAGE

The following plants occurring as families and colonies in a very open stand constitute the remarkable pioneers on the loose coarse sands. They are arranged roughly in order of frequency of occurrence. Detailed account of some of these especially interesting plants will be given later. So widely are these plants commonly spaced, that dominance of one species seldom occurs; competition for nutrients and possibly for water may, however, be going on.

Alsinopsis Caroliniana, Asclepias humistrata, Breweria humistrata, Cladonia sylvatica, Cuthbertia rosea, Dasystoma pectinata, Dasystoma Pedicularia, Pinus palustris, Polygonella polygama, Quercus Catesbaei, Selaginella acanthonota, Stipulicida setacea, and *Tithymalopsis Ipecacuanhae.*

OBSERVATIONS ON PIONEER PLANTS

So remarkable are the pioneer species which can enter the very dry surface soil of the coarsest sand, that a few of them will be discussed in some detail to bring out the wide variation, which is to be observed among them, particularly in root conditions. The adaptations to this xeric habitat of edaphic origin have evolved in many different directions.

Cladonia sylvatica. This lichen is distributed in clumps and masses of varying size (Fig. 1) and is attached basally to small quantities of organic débris, the whole being free from the sand, for the masses may readily be moved about by the foot. In many pioneer sites of pure white coarse sands, this lichen is associated with *Selaginella acanthonota,* filling the central part

of the radially expanding Selaginella colony (Fig. 2). The studies of Porter and Woolet (9) on Cladonia and its influence on soil moisture are of in-

FIG. 1. Cladonia consocies near White Lake.

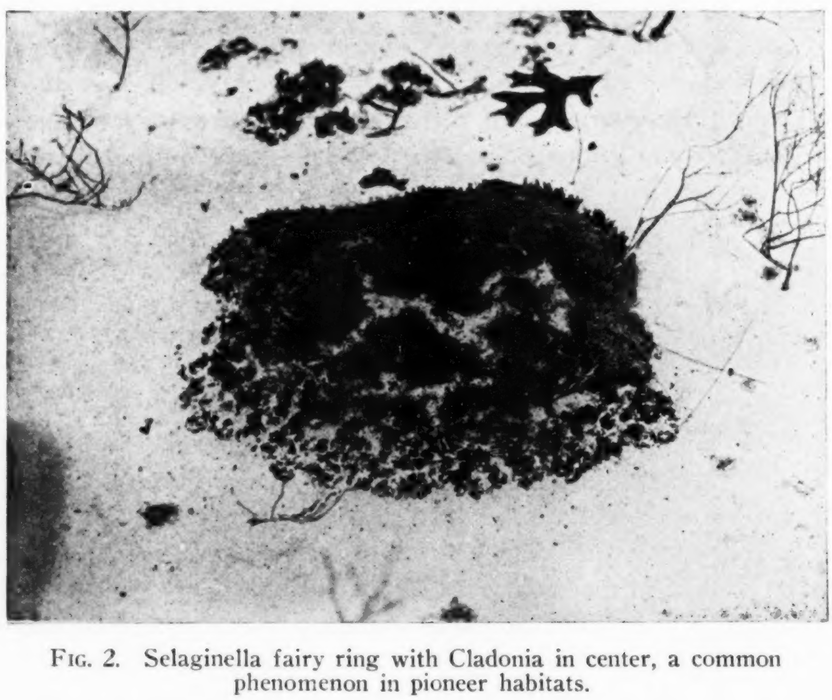

FIG. 2. Selaginella fairy ring with Cladonia in center, a common phenomenon in pioneer habitats.

terest in this connection. They found that Cladonia mats kept the soil moisture slightly above that around them and exerted a more marked effect

in almost totally absorbing the water of light rains and dew. Thus Cladonia cannot be regarded as a type of vegetation contributing much of anything to the improvement of the soil water status of the surface layer.

Stipulicida setacea. This interesting shallowly rooted little annual known as the "wire plant" from its very slender, delicate, wire-like stems, has solved

FIG. 3. Wire plant *(Stipulicida setacea)*, an annual pioneer.

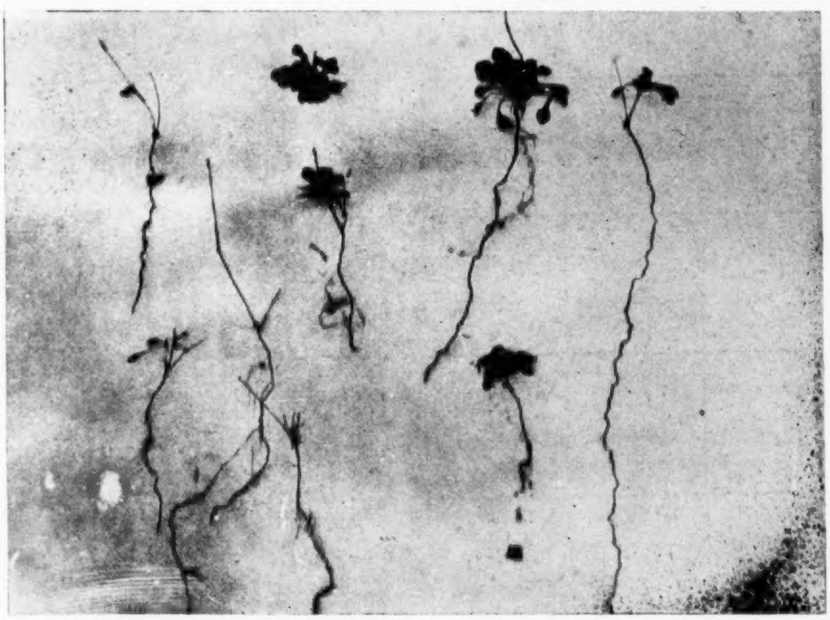

FIG. 4. *Stipulicida setacea.* Spring aspect showing rosettes of leaves which disappear before summer.

the problem of this extreme habitat by carrying out its vegetative activity in the early spring period when both soil water and humidity conditions are more favorable. By midsummer all the food making leaves of its basal

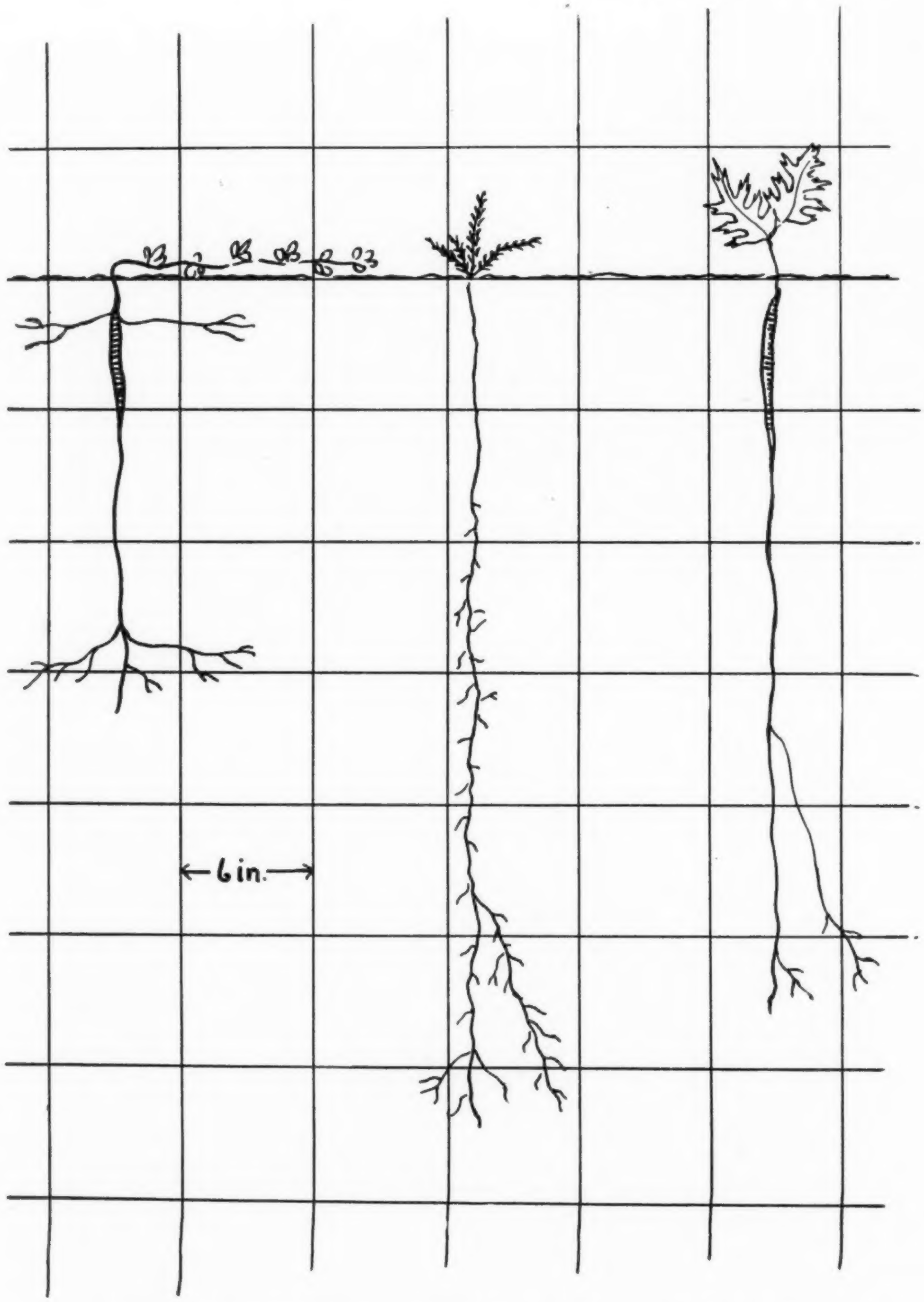

FIG. 5. Root distribution. *Galactia* sp. left, *Alsinopsis Caroliniana* middle, *Quercus Catesbaei* right.

rosette are gone and the plant is in flower and fruit. The hot months of July, August, and September are spent in the seed stage—a habit of many desert plants (Figs. 3, 4).

FIG. 6. Juvenile turkey oak *(Q. Catesbaei)* showing vertical orientation of leaves.

Quercus Catesbaei. The root of this tree in the juvenile stages is strictly of the tap root type being, elongate tuberous at its upper end (Fig. 5). The stem arises from the upper end of this tuber which is always buried one or more centimeters in the soil. The tuber undoubtedly functions as a water storage organ. The acorns of this oak furnish ample food for a deeply penetrating primary root the first season.

Of especial interest is the peculiar leaf orientation of this oak. In the juvenile stages and to a less degree when larger, the turkey oak orients the plane of its leaf blade vertical to the ground surface (Fig. 6). This vertical orientation of the leaf blades is a well known xeric character, since the temperature of the leaf is kept lower than would be the case if the leaf absorbed the radiation. In white sand with reflected radiation this character would have an increasing significance.

During two spring seasons tests were made by holding a number of juvenile plant leaves located within a few inches of the ground in a horizontal position with the aid of wire (Fig. 7). After a moderate drouth or inter-rain period these leaves displayed a yellowish green color in contrast to the controls, or leaves of the same plant left vertically oriented. The evidence indicated that during an extended drouth of an exceptional year genuine injury would result from the enforced horizontal position. It

may be concluded that the vertical orientation of the leaves of *Quercus Catesbaei*, especially in the juvenile stages is a valuable character in enabling the plant to establish itself in deep loose sand. In this connection it is of interest to call attention again to the fact that this species is the only broad-leaved tree able to come in on the pioneer sites.

The cross section of the leaf (Fig. 8) shows the presence of a very thick upper epidermis and moderately thick under epidermis. The spongy layer is rather compact. These characters, together with the one of leaf orientation, are all xeric adaptations.

FIG. 7. Juvenile turkey oak with one leaf horizontally oriented by wire, resulting in yellowing.

This oak is also prominent in the xeric phase of the Aristida consocies where it is far more subject to fire than in the bare areas of pioneer sites with no ground cover to carry fire. With its thick deeply ridged bark it is rather resistant to fire. The trunk may remain uninjured when the branch tips are injured. The trees thus frequently show a narrow columnar-shaped crown due to this type of fire injury. Of especial significance, of course, is its well known habit of regeneration by basal shoots. Most areas thus show the oak trunks in groups of twos and threes for the existing trees are almost all regeneration forms on the fire swept areas.

On slopes as the water table is approached it is found that this oak never occurs as close to the water table as the black jack and the other more mesic species.

The turkey oak leaves during the summer and fall become badly mined

by a lepidopterous leaf miner. This widespread condition gives the trees a characteristic aspect at this time of year.

Pinus palustris. The southern pines are all xeric in nature and it is not surprising to find the long leaf pine able to enter the pioneer or bare sand areas. The large seed of this species is to be correlated with the establishment of the seedling one year pine. Not only is it able to hold more water but the original content of nutrients is sufficiently large to carry the primary root a long distance to the more stable water supplies below. For a discussion of establishment and other important features of this species, see Mattoon (7) and Pinchot and Ashe (8).

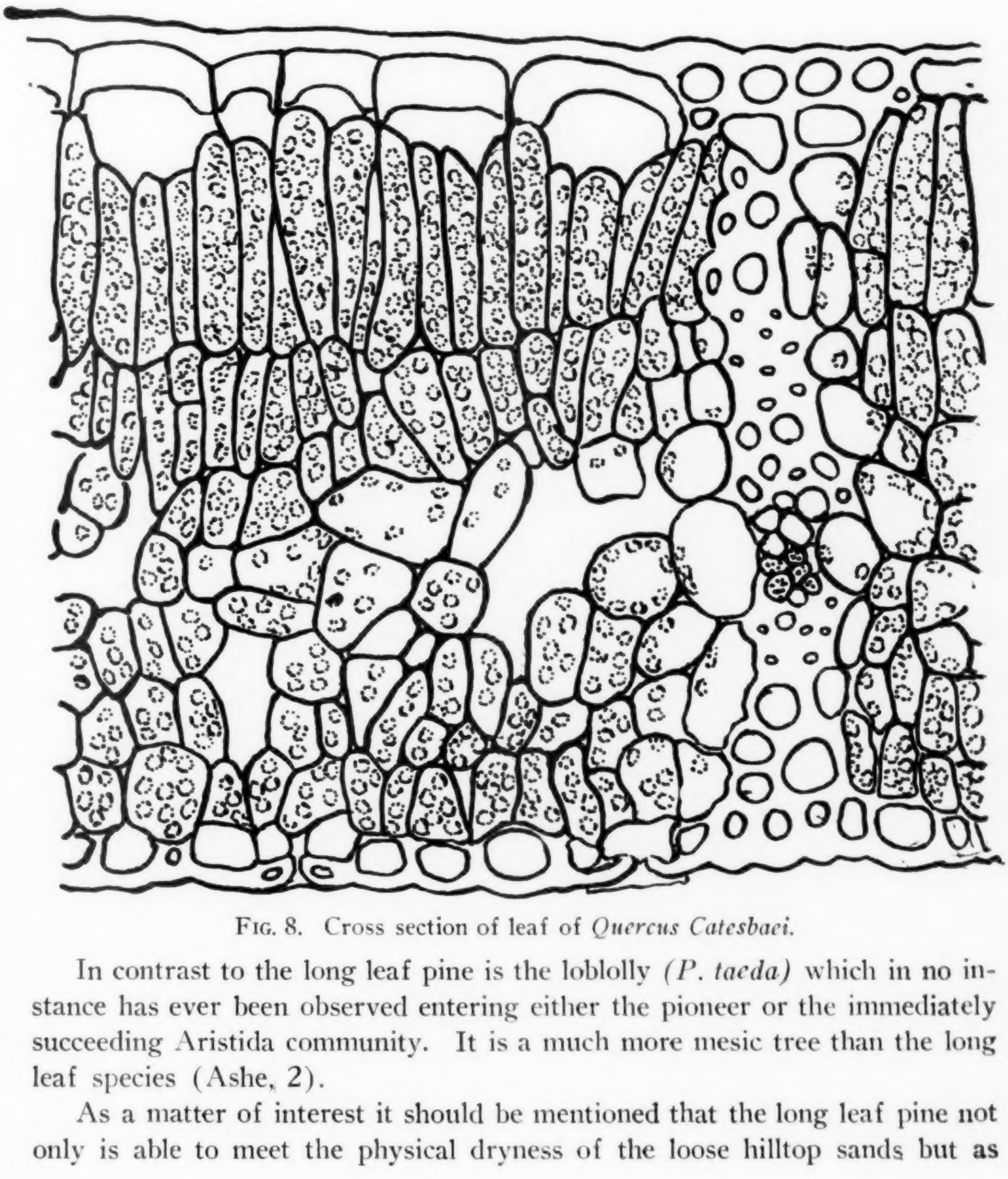

FIG. 8. Cross section of leaf of *Quercus Catesbaei.*

In contrast to the long leaf pine is the loblolly *(P. taeda)* which in no instance has ever been observed entering either the pioneer or the immediately succeeding Aristida community. It is a much more mesic tree than the long leaf species (Ashe, 2).

As a matter of interest it should be mentioned that the long leaf pine not only is able to meet the physical dryness of the loose hilltop sands but as

shown in our transect (p. 486, Fig. 18) sketch it appears and succeeds in bog areas where fire has eliminated the shade of shrub bog and transformed it into grass-sedge bog. Such an area was near our transect and young *P. palustris* was appearing on it in soil which is kept perennially wet. Thus the long leaf pine may be said to have a wider range (for it grows well in mesic habitats free from competition) in its water relations than any other southern tree. This fact makes this woody species valueless as an indicator plant.

Other Tap Root Types. *Alsinopsis Caroliniana* (Fig. 5) and *Tithymalopsis Ipecacuanhae* both early put down long primary roots. In the latter this root while young thickens through most of its length and becomes a water- and food-storage organ. Compared to the small vegetative rosette at the surface, the spurge possesses in deep sand an extraordinarily long and thick root. One specimen partly dug out, having a rosette of stems and leaves 8 inches wide, possessed a root which at the six foot depth was 1 cm. thick.

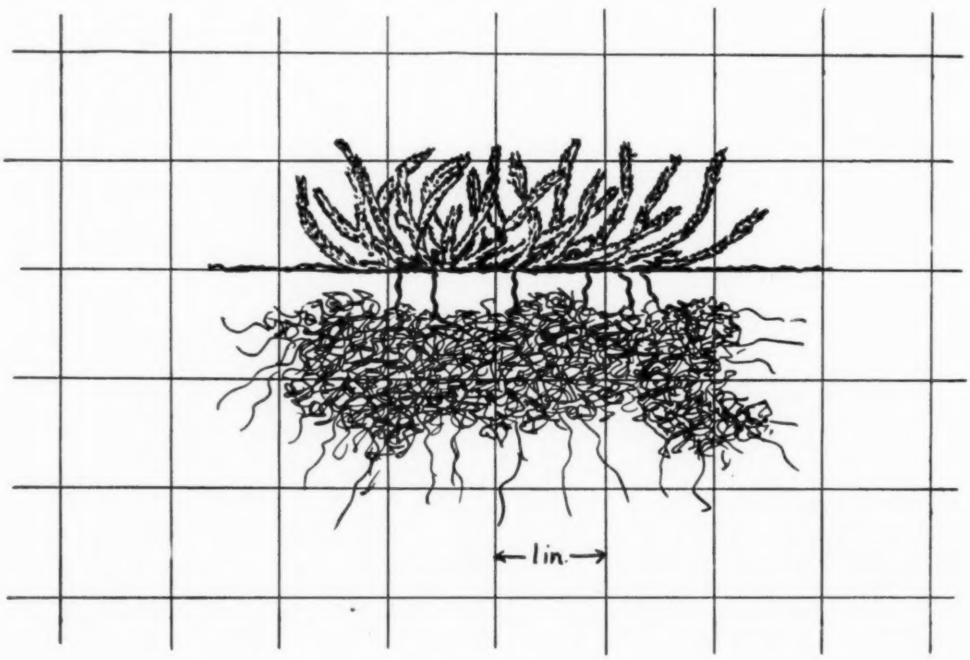

FIG. 9. Root distribution. *Selaginella acanthonota.*

Selaginella acanthonota. This heterosporous fern unlike most selaginellas has very small, scale-like, thickly imbricated leaves on short incurled branches (Fig. 2). In its root structure is to be observed a most unusual adaptation. Fine primary roots, few in number, descend from the horizontally oriented stems and a centimeter below branch most profusely into a close almost compact net-work of extremely fine rootlets which are to be ranked as among the smallest roots (diameter measurement) known. This compact sponge-like mass of rootlets is 3-5 cm. thick and extends merely throughout the area occupied by the surface vegetative structures (Fig. 9).

No other plant was found at any stage of the sere with a root system like that of Selaginella; it appears to be unique.

Dasystoma. The two species of this genus *(D. pectinata* and *D. Pedicularia)* are the broadest leaved herbaceous pioneers found. *D. pectinata* has the

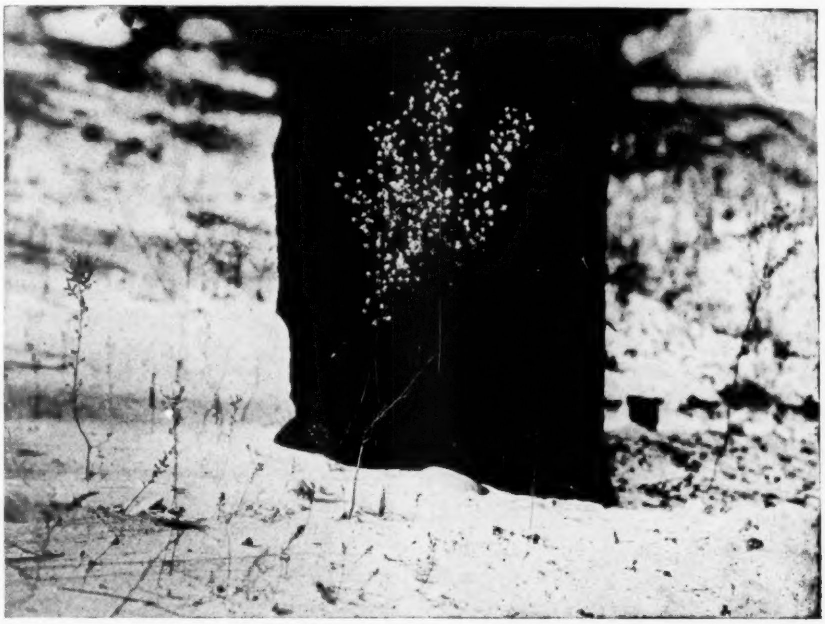

FIG. 10. *Polygonella polygama,* a pioneer, flowering in midsummer after self-defoliation.

FIG. 11. Bare area near White Lake with *Polygonella polygama* entering.

largest leaves and these are covered with a viscous, glandular secretion which probably functions in the prevention of water loss. The fact that these plants as annuals reach the size they do (2-2½ ft. high) in these sterile dry soils, makes them outstanding in interest. However, it was not possible at the present time to study them intensively. Small nodules are present on the roots of *D. pectinata.* The function of these is unknown.

Polygonella polygama. This plant, a perennial by a woody base, is especially noteworthy because of its habit of dropping its leaves at flowering time in early summer (Fig. 10). The extremely hot season of late summer is also passed in a leafless state, a characteristic which may be observed in many desert plants. This species has in a few instances been observed to be the first and only pioneer on newly created bare areas in coarse sand (Fig. 11).

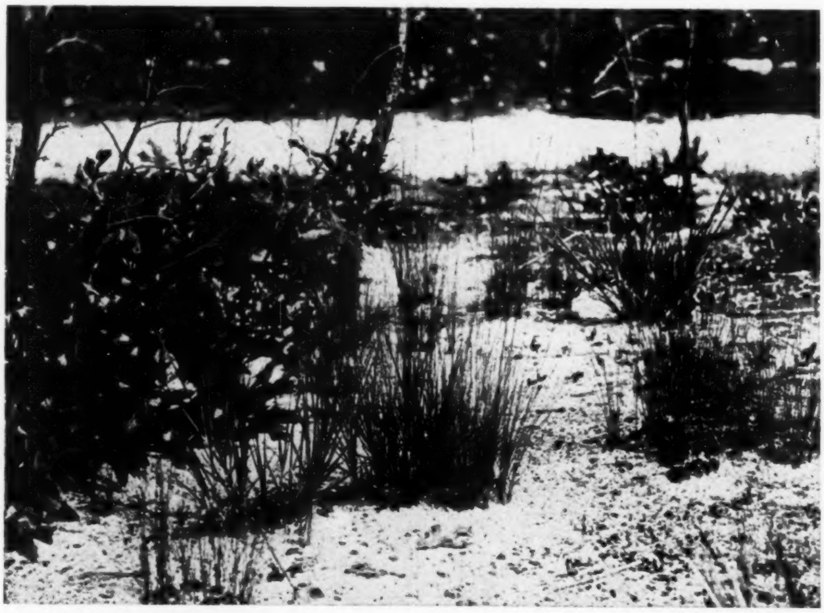

FIG. 12. Wiregrass *(Aristida stricta)* the dominant and indicator of the sandier soils under fire. Note the stiff erect habit of the fine leaves.

XERIC PHASE: ARISTIDA CONSOCIES

Attention should be called to the fact that all of the pioneers except Selaginella and Polygonella may be found associated with Aristida. In no instance have these two ever been seen to occur in a well developed Aristida community. The others while they persist in the less xeric habitat, are not included to save repetition. In the following list, the plants starred have been reported by Small in "dry sandy soil" from North or South Carolina, but have not been collected by us.

Afzelia pectinata, Anastrophus compressus,* A. paspaloides,* Aristida Chapmaniana,* A. stricta, Asclepias aceratoides, A. amplexicaulis, A. hu-*

mistrata, A. Michauxii, Ascyrum stans, Asimina parviflora, Aster elodes, A. gracilis,* A. spectabilis,* Baptisia microphylla,* B. perfoliata,* B. villosa, Carduus repandus, Carex chapmanii,* Carphephorus bellidifolius, C. corymbosus, Chenolobus undulatus, Chrysopsis graminifolia, C. Mariana, C. pilosa, Cnidoscolus Virginiana, Dasytephana Porphyrio, Dicranum spurium, Diospyros Virginiana, Epigaea repens, Eriogonum tomentosum,* Galactia erecta, G.*

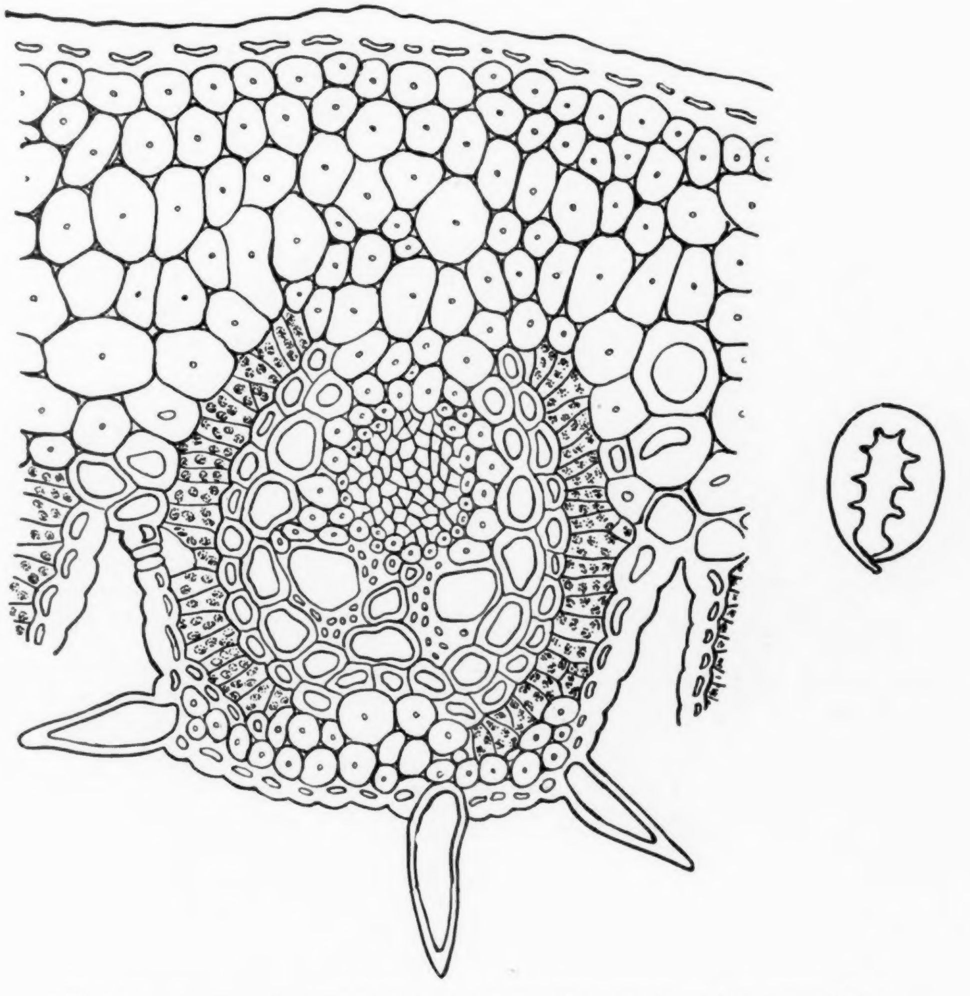

FIG. 13. Cross section of leaf blade of *Aristida stricta*. Note excessively large amount of lignified cells.

regularis, G. sp., Gaylussacia dumosa, Helianthus glaucus, Kneiffia arenicola, Kuhnia paniculata, Kuhnistera pinnata, Lupinus diffusus, L. perennis, Onosmodium Virginianum, Opuntia opuntia, Phaseolus sinuatus,* (1 specimen only. Far from its range: Fla.-La.), *Pinus palustris, Podostigma pedicellata, Psoralea Lupinellus, Pyxidanthera brevifolia, Rynchospora dodecandra, R. Grayi, Sabbatia angustifolia, Silphium pinnatifidum, Sisyrinchium sp., Stenophyllus capillaris, Stillingia sylvatica, Stylosanthes biflora, Tithymalopsis*

*gracilis, Tithymalopsis Ipecacuanhae, Tium apilosum, Tragia urens, Triplasis Americana,** and *Zornia bracteata.*

Only a few species of the Aristida consocies xeric phase need be discussed in detail.

Aristida stricta. This remarkable grass (Fig. 12), the accurate indicator of medium to coarse sand in all upland soils including semi-bogs under fire, is a very xeric grass. In thin stand it has very erect tenuous leaves, the tiny blades of which are folded together ventrally, so that one margin tightly overlaps the other. This structure is early assumed in growth from the stooling base and there is a deposition of large quantities of lignin and cellulose (Fig. 13) in all the tissues except the chlorenchyma and phloem. The leaf becomes very rigid indeed for its small diameter and is chiefly composed of fibers.

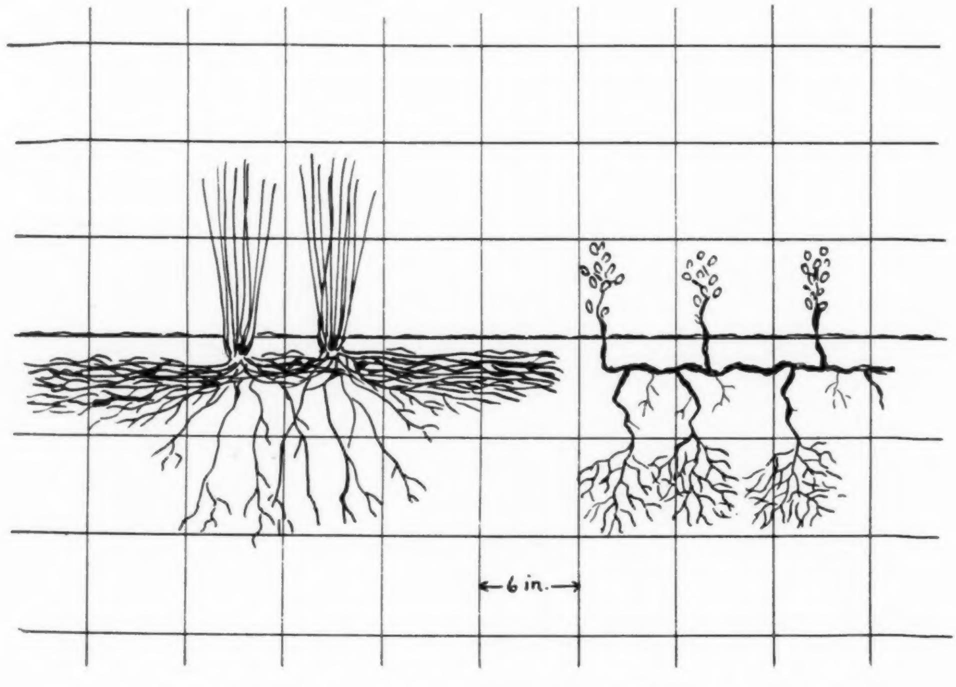

FIG. 14. Root distribution. *Aristida stricta* left, *Gaylussacia dumosa* right.

The roots are relatively thick for fibrous grass roots and in deep sand are oriented chiefly in the surface 4 inches of soil (Fig. 14). It is probable that these roots are essentially of the tuberous type and serve as water reservoirs when the surface soil is air dry, as it may be for extended periods. Only when the water table is within a few feet of the surface do roots descend deeper than a foot. The dark humus layer (⅓ in. thick) found in Aristida consocies areas are built chiefly from Aristida roots. It was observed that on slopes tussocks which had a portion of their superficial roots washed out uniformly died.

Gaylussacia dumosa. This plant in many localities is a successful competitor with Aristida, forming socies generally and only rarely appearing as a consocies. Its leaf is not an extreme xeric type. The thick cutin on the upper side is probably significant (Fig. 15). Roots (Fig. 14) occupy a different zone of soil than those of the wire grass, with which Gaylussacia is

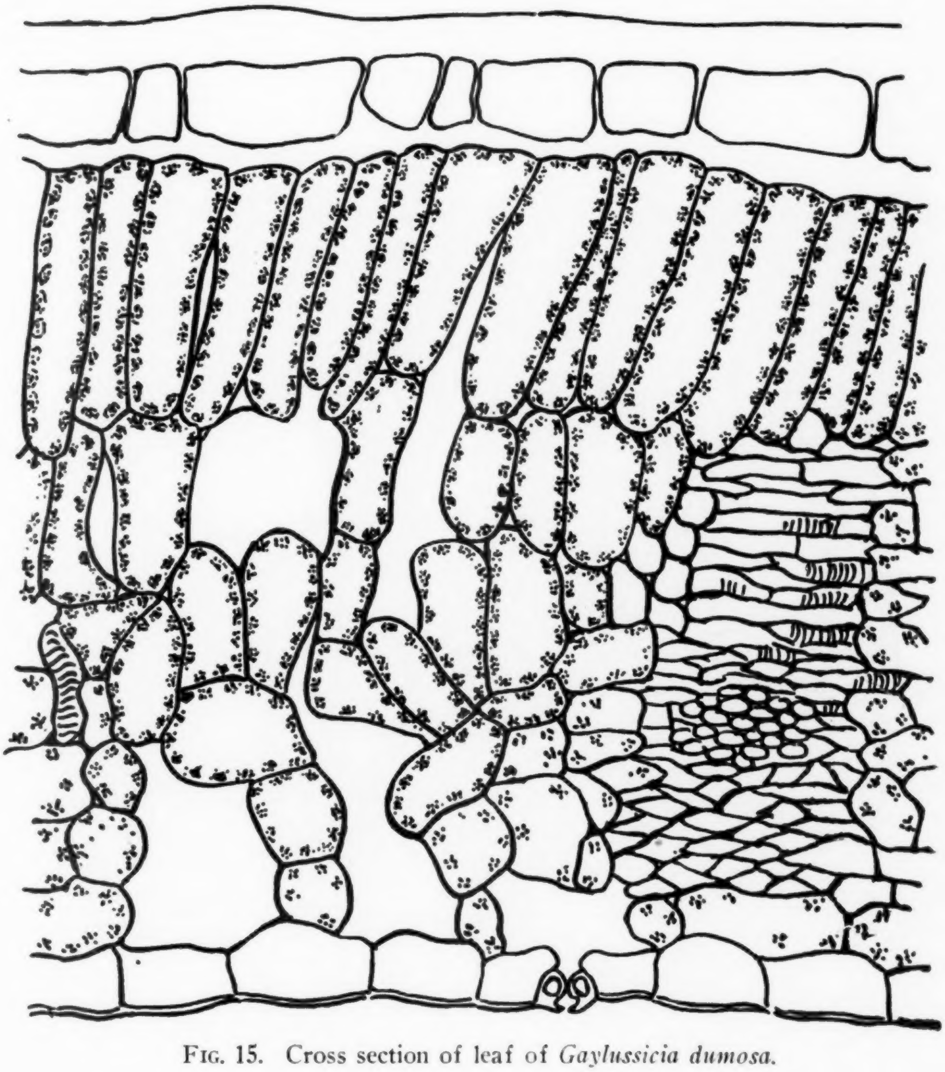

FIG. 15. Cross section of leaf of *Gaylussicia dumosa.*

commonly associated in a mixed community. The less xeric character of the leaf is to be correlated with the deeper root system. It was observed that the running huckleberry was more tolerant of shade than Aristida, hence socies of this species are apt to appear when the scrub turkey oaks become closely spaced.

Galactia. The Galactias of which certain specimens are as yet unassignable to particular species, constitute a characteristic trailing type in the open

Aristida areas. These have a well developed tuberous tap root of high water storage capacity (Fig. 5).

Pyxidanthera brevifolia. This plant (Fig. 16), a new species discovered and described during the course of the writers' studies appears to have a remarkably restricted distribution. Frequent, and in places common, in its type locality near Spout Springs, it occupies an area so far as known not over six miles square. It is the xeric phase representative of the genus while the only other and related species *(P. barbulata)* is found in the semi-bog phase of the consocies. The plant appears to be a relict species surviving today wholly on a basis of vegetative growth. Examination of the seeds

FIG. 16. *Pyxidanthera brevifolia.* Rare, xeric new species found in southern Harnett County, sandhill area.

showed only a few which could be regarded as normal in shape and size and these we have been unable to germinate. Careful search for seedling plants in the field yielded no results. This species thus takes its place among those rare plants like *Gaylussacia brachycera* which are holding on in a few local stations through vegetative activity alone.

It is of passing interest to note that this plant belongs to the *Diapensiaceae,* a family which includes only a few species, many of which are rare or of restricted distribution. The rare genus Shortia of the southern Appalachians belongs here.

Dicranum spurium. This is the one moss observed in the Aristida consocies, xeric phase. In this consocies it is confined strictly to the shaded areas beneath the turkey oaks.

Epigaea repens. The abundance of trailing arbutus in the hot, open scrub of the Sandhills is a notable example of a plant which apparently thrives out of its typical habitat, the mesic forest. Xeric in nature and finding its peculiar soil demands fulfilled in the Aristida humus infiltrated soil, it is surprisingly abundant in many places where the fire hazard is not too great because of a thin stand of wire grass.

XERO-MESIC PHASE: ARISTIDA-QUERCUS (MARYLANDICA) MICTIUM

This phase may be readily distinguished in the field by the presence of black jack oak *(Quercus Marylandica)* and the absence of hickory. In addition to species of the preceding xeric community which tend, under the open stand of the black jack oak trees, to freely enter the more mesic habitat, we have observed the following species to accompany the characteristic oak of this phase:

FIG. 17. *Opuntia opuntia.* Cactus species in xero-mesic phase of Aristida consocies.

Amorpha herbacea, Amsonia ciliata, Andropogon capillipes, A. perangustatus, Aristida purpurascens, Ascyrum hypericoides, A. multicaule, Ceanothus intermedius, Cracca ambigua, C. Virginiana, Crataegus uniflora, Crotalaria rotundifolia, Cyperus hystricinus, Dendrium buxifolium, Diospyros Virginiana, Dolicholos simplicifolius, Gaylussacia frondosa, Hieracium Marianum, Hyperium canadense, Liatris punctata, Lobelia Canbyi, Meibomia arenicola, M. tenuifolia, Monarda punctata, Morongia uncinata, Myrica Carolinensis, Opuntia opuntia, Panicum angustifolium, P. arenicola, P. Nashianum, P. sphaerocarpon, Phlox Hentzii, Physalis lanceolata, Pieris Mariana, Poly-

premum procumbens, Quercus brevifolia, Q. Margaretta, Q. Marylandica, Rhus toxicodendron, Robinia nana, Salvia lyrata, Sassafras sassafras, Solidago odora, Spermolepis divaricatus, Tithymalopsis Curtisii, Vaccinium Myrsinitis, V. tenellum, and *Verbena Carolinensis.*

The black jack oak in the juvenile stage possesses a tuberous tap root similar to that of the turkey oak. Vertical orientation of the leaves also occurs at this time.

Robinia nana seldom grows over 18 inches high. It has highly functional leaflet pulvini, for these organs move every 24 hours through an orbit of 180 degrees. During the day the leaflets are stiffly erect and lie face to face; at night they drop to the fully pendent position. This movement is wholly phototropic in nature; the leaves could be made to droop during the day by covering the plants.

The blue-jack oak *(Q. brevifolia)* and Margarett's oak *(Q. Margaretta)* are slightly more mesic than the black jack, hence never extend into the turkey oak areas as far as the latter.

The fetterbush *(Pieris Mariana)* is a sure indication of very favorable water conditions wherever this occurs with the black jack oak.

It is on land formerly occupied by this consocies that the peach orchards are chiefly located. In this connection it is of interest to note that the peach tree is xero-mesic in nature for it not only has a relatively low rate of transpiration (Kelly, 4) but its leaves hang downward from the branches in such manner as to escape the direct incidence of the midday light and heat rays.

MESIC PHASE: ARISTIDA-HICORIA MICTIUM

This phase is of very restricted distribution and is generally confined to a narrow zone on hillsides a few feet above the water table. The presence of small hickories *(Hicoria alba)* is characteristic of this phase. Accompanying the hickory are a few other woody plants which are not seen in the black jack-turkey oak zones. These are: *Andropogon Elliotii, Andropogon Virginicus, Batodendron arboreum, Batodendron corymbosum, Ceanothus Americanus, Hicoria alba, Polycodium candicans,* and *Rhus copallina.*

No true mesic herbaceous plants such as the herbs found in a mature oak-hickory forest are ever present; the ground cover consists chiefly of wire grass accompanied by other plants of the two preceding phases.

In most situations, it is very probable that the mesic woody plants are frequently relicts following fire. In close stand such a mesic community would eliminate the xeric grasses and other plants by shading. Hence the mesic phase involves highly restricted areas, always on slopes where the wire grass stand is broken by washing. On level areas the luxuriant wire grass furnishes such a fire hazard that mesic shrubs and trees, even though they were successfully tending to come in, would be as quickly eliminated.

SEMI-HYDRIC OR SEMI-BOG PHASE: ARISTIDA CONSOCIES OF THE CAMPULOSUS-PANICUM ASSOCIES

This community is one of much interest for it represents the presence in the same habitat of plants which commonly demand very different water relations. Coarse sand areas of low relief having a high water table for extended periods alternating with depressed water table in drouth years, constitute the habitat of this community.

A glance at the following list will show the interesting fact that of the xeric and mesic phase herbs, only the wire grass *(Aristida)* is present. And it is dominant if the average hydro-period is not too long when the orange grass *(Campulosus)* and many other full grass-sedge bog plants will be found. The long leaf pine also occurs here. This community thus forms ir the coarser sands a transition or semi-bog phase.

Some of the more frequently seen species in this phase are:

Afzelia cassioides, Aristida stricta, Dionaca muscipula, Eupatorium leucolepis, Hypericum aspalathoides, Juncus scirpoides, Koellia aristosa, Lacinaria Wellsii, Lobelia Nuttallii, Oldenlandia uniflora, Panicum virgatum, Pinus palustris. Polygala lutea, Pyxidanthera barbulata, Rhexia Alifanus, R. ciliosa, Rynchospora Torreyana, Scleria triglomerata, Sericocarpus bifoliatus, Sporobolus ejuncidus, Thyrsanthema semiflosculare, Trilisa odoratissima, T paniculata, Vaccinium crassifolium, Xyris brevifolia, and *X. flexuosa.*

Probably most of the plants listed under the Panicum consocies or semi-bog plants in our earlier study (13) may at one place or another be associated with wire grass. Our theory of the complex of changing factors making possible such a unique consocies will be given later in the portion of the article devoted to discussion.

The foregoing four phases of the Aristida community not only indicate medium to coarse sand but fire as well and, since fire is universal, the sand-hill uplands with but the rarest exceptions are vegetatively some phase of the Aristida consocies. The pioneer stage of the prisere does not involve fire since the bare sand areas are too extensive to carry ground fires. Crown fires are almost unknown.

A glance at Fig. 18 which is a diagrammatic treatment of the plant distribution on one hill slope transect near Sprout Springs, Harnett County, North Carolina, will bring out the relation of the foregoing phases. Note the dependence of the xero-mesic black jack oak on the higher water holding capacity of the clay layers; the position of the hickory zone above the permanent water table; the very interesting development of shrub bog (Fig. 19) on the lower slope due to seepage from the surface of the lower terrace—forming layer which creates a permanent elevated water table; the wide range of long leaf pine found in every situation except the swamp forest site.

Pinus palustris consocies. Among the fire subclimaxes must be included

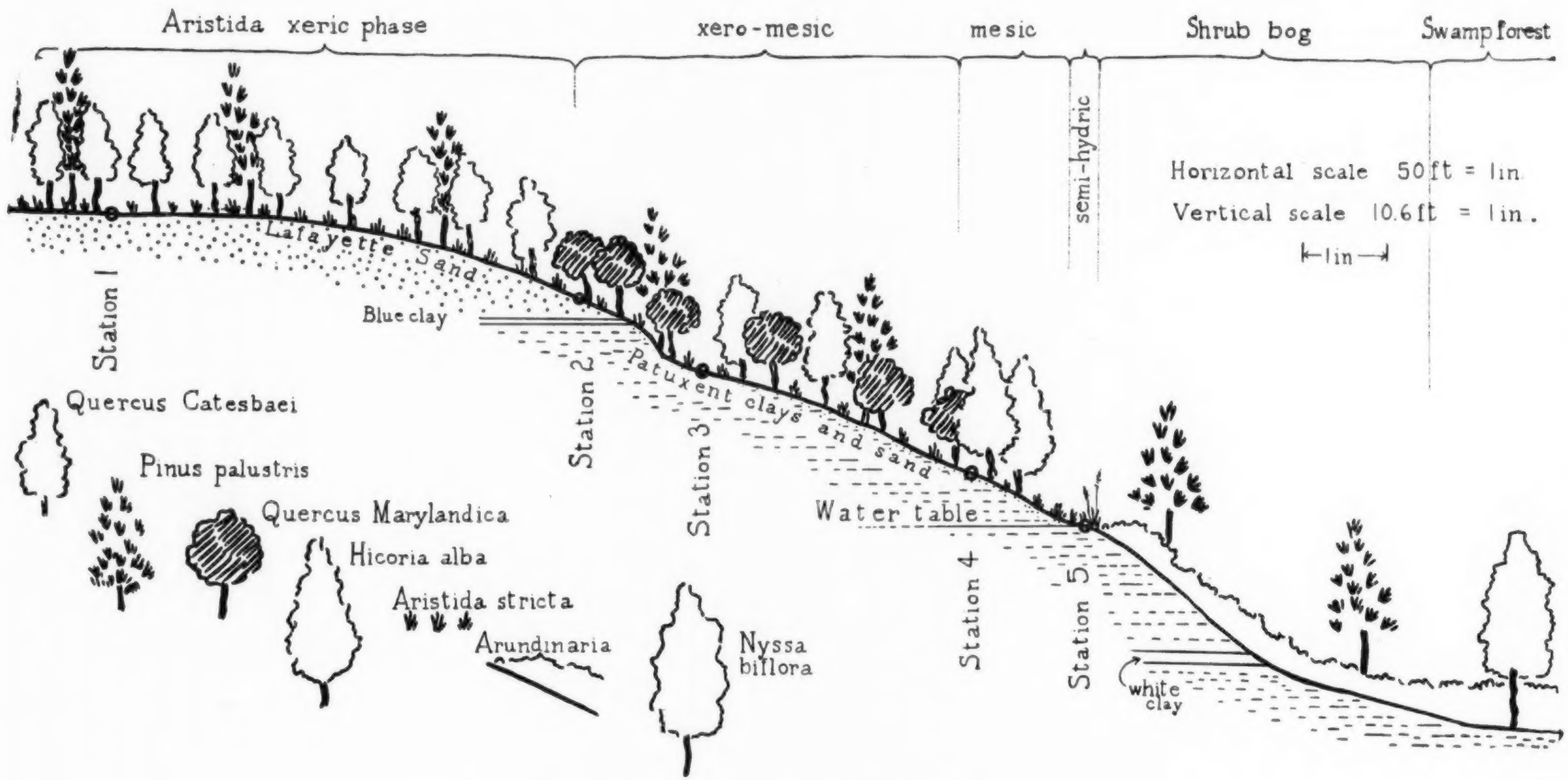

FIG. 18. Spout Springs transect. Total relief 65 feet. Vertical scale exaggerated about five times that of the horizontal.

one now seldom seen because of fire, severe cutting and turpentining; viz., the long leaf pine forest in close stand. Surviving fire (if not too intense) as no other tree in the region does, it, in time without interference on man's part, may develop dominance on areas occupied by any of the Aristida consocies phases. Through the shade effected in close stand together with the smothering effect of the needle accumulations during years without fire, herbaceous vegetation and to a large degree the shrub cover as well may be held in check.

FIG. 19. Contact of wire grass and shrub bog showing sharpness of transition. No broom sedge zone is present. Spout Springs transect.

It was such a fire subclimax that the earliest white men found when they reached the areas of the coarser sands. The description of a pioneer in the Sandhills has already been given. John Washington writing from Lenoir County in 1810 describes the "long leaf pines on the sandy land south of the "Neuse" while north of the river on the finer soils were oak, hickory, dogwood, and short leaf (loblolly) pine." In its pristine condition with millions of trees measuring a yard or more in basal diameter, the *Pinus palustris* consocies unquestionably presented one of the most wonderful forests in the world. And today hardly an acre is left in North Carolina to give its citizens a conception of what nature had wrought in an earlier day. The complete destruction of this forest constitutes one of the major social crimes of American history.

It has been noted that in the rare stands of virgin long leaf pine which have been observed that the flowering dogwood *(Cynoxylon florida)* is the

shrub which is prominent as the understory plant. This shrub is probably the most successful of mesic, woody, broad-leaved plants in fire resistance.

It is thus evident that sufficiently frequent fires occurred in the coastal plain to maintain this area largely as a pine fire subclimax.

In this connection it is of the greatest importance to know that fire was not uncommon during prehistoric days. Evidence for this is very clear from old records. The descriptions of savannahs or grass sedge bogs are frequent and since this community cannot come into existence or be maintained without fire, this alone is conclusive evidence of fire. Lawson (5) in his history of North Carolina in an account of travel with some Indians states: "I perceived these Indians were in some fear of enemies for they had an old man with them who was very cunning and circumspect, wherever he saw any marks of footing or of any fire that had been made; going out of his way very often to look for such marks." In another place he mentions a fire as follows: "We travelled about twenty miles lying near a savannah that was overflown with water: where we were very short of victuals but finding the woods newly burnt and on fire in many places which gave us great hopes that Indians were not far off. Next morning we waded through the savannah."

Quercus Virginiana consocies. This community may be observed only near the coast, particularly where the mainland fronts on the sea. Very many species of the Aristida consocies plants are to be found in it. Neither Q. Catesbaei or Pinus palustris occur in the seaside margin of the community. The old pines first in from the ocean are uniformly highly distorted, the trees changing their aspect completely under the influence of the wind factor which is of primary significance in the differentiation of this consocies.

The Sere: Successional Relations

The kind of communities which would appear in time on these various areas of differing native soil water content, without the destructive effects of fire ever occurring, must be largely speculative. Practically no areas of even the most restricted size can be found where fire has not recently initiated a subsere. However, on a basis of fundamental ecological principles together with the very meager field data available, the following bare outline of the non-pyric subsere has been formulated.

Quercus Catesbaei consocies. The appearance of the turkey oak as a true dominant is wholly related to absence of fire. Even under fire this species holds on in a repressed condition through its well known habit of regeneration by basal shoots. It is thus already present today over vast areas and ready to attain size and dominance with fire cessation. The wire grass will persist for a long time since the tendency of the oak leaves to orient themselves vertically, a character so marked in the first years of growth, still is evident. And being so deeply lobed in addition, the shade factor is of low intensity.

Quercus Marylandica consocies. With the accumulation of leaf litter and its well recognized mulching effect in checking soil water evaporation, the water content of the soil could be maintained over the long drouth periods at a point where the juvenile black jack oak would survive. This xero-mesic tree with its heavier shade would in time become dominant and pave the way for the final mesic forest.

Hicoria alba consociation. From evidence to be presented later under the discussion of habitat factors, it is believed that a mesic forest representing the climax of the Eastern United States Region, could only appear, if at all, after centuries without fire. Such a mesic forest would probably be chiefly represented by the mockernut hickory as already indicated. At the present time there is practically no beech-maple forest present in sandhill country. Following many centuries of fire control this forest should come in along the valley slopes, but in our opinion the appearance of this extreme mesic community on top of the hills with deep coarse sand would never occur.

From the foregoing it has been seen that the oaks differ in their soil water relations. The principal oaks of the sandhill region may be arranged in order from the most xeric to the most mesic in the following sequence: *Q. Catesbaei, Q. brevifolia, Q. Marylandica, Q. Margaretta, Q. stellata, Q. falcata, Q. coccinea, Q. velutina,* and *Q. alba.*

Old Field Succession. One of the most peculiar facts to be noted in the response of vegetation to habitat changes is that related to the flora coming in following the abandonment of cultivated areas. Outstanding is the observation that the wire grass does not return. Areas abandoned as much as 15 years ago show no wire grass; the transition from the weed flora to the adjoining native wire grass cover is as sharp as the plow furrow which broke the original wire grass sod. Consistent search for an abandoned field or orchard in the extensive sandhill area in which there was evidence of the return of Aristida failed to disclose any.

The pioneer Cladonia consocies areas are never cultivated so there is not the same problem here. On the xeric and xero-mesic sites, however, a weed succession differing very much from that of the very familiar mesic crabgrass—tall weed—broom sedge prisere is found. On the drier sands an open stand of the following depauperate weeds appears: *Adopogon Carolinianus, Aristida purpurascens, Cyperus cylindricus, C. rotundus, Diodia teres, Dolicholus simplicifolius, Gymnopogon ambiguus, Isopappus divaricatus, Kneiffia linearis, Lechea Leggettii, Leptilon canadense, Lespedeza capitata, Lespedeza hirta, Panicum sphaerocarpon, Polypremum procumbens, Rumex acetosella,* and *Sarothra gentianoides.* Among these the most common is the horseweed or Canada fleabane (Leptilon canadense). It is to be observed attaining a widely varying stature and may thus be used as an ecad in measuring certain fundamental characters of the soil habitat. In the lower areas with mesic conditions prevailing, whatever the cause, the usual weed flora

common elsewhere obtains with crab grass *(Syntherisma sanguinale)* dominant at first, followed by a number of the familiar tall weeds. Carpet weed *(Mollugo verticillata)* is also a pioneer holding its own readily even in cultivated orchards.

Present also in fields long abandoned (5 years or more) are a number of the native species which unlike the dominant wire grass are able quickly to enter these areas and successfully compete with the ruderal vegetation. The following have been especially observed: *Asclepias humistrata, Carduus repandus, Chrysopsis graminifolia, Pinus palustris, Stipulicida setacea,* and *Tragia urens.*

FIG. 20. Good regeneration of long leaf pine in an old field. Site favorable for water. On slope of "Blue's Mountain," a high hill in Cumberland County.

In contrast to these, certain other plants seemed entirely incapable of ecesis in the old field habitat. Though growing abundantly immediately next to the broken ground and in one instance having had 15 years in which to extend their local range, no instance of their appearance was noted. Such plants were: *Aristida stricta, Dasystoma pedicularia, Galactia sp., Gaylussacia dumosa, Lacinaria punctata,* and *Stillingia sylvatica.* Why these, especially the wire grass, are not able to reappear in land once broken, cultivated, and abandoned is not known. Since pines may come in (Fig. 20) it is possible that in such areas the pine subclimax, is reached without going through a wire grass stage. A summary of the successional relations is given in Fig. 21.

HABITAT

As already clearly indicated, the medium to coarse upland sands under the present climatic conditions of the southeastern United States constitute the particular habitat of the xeric associes treated herein (Figs. 22, 23). The soils concerned are recognized in the United States Bureau of Soils classification as Norfolk sand, Leon sand, and St. Lucie sand. In many places part of what is called Portsmouth sand should also be included.

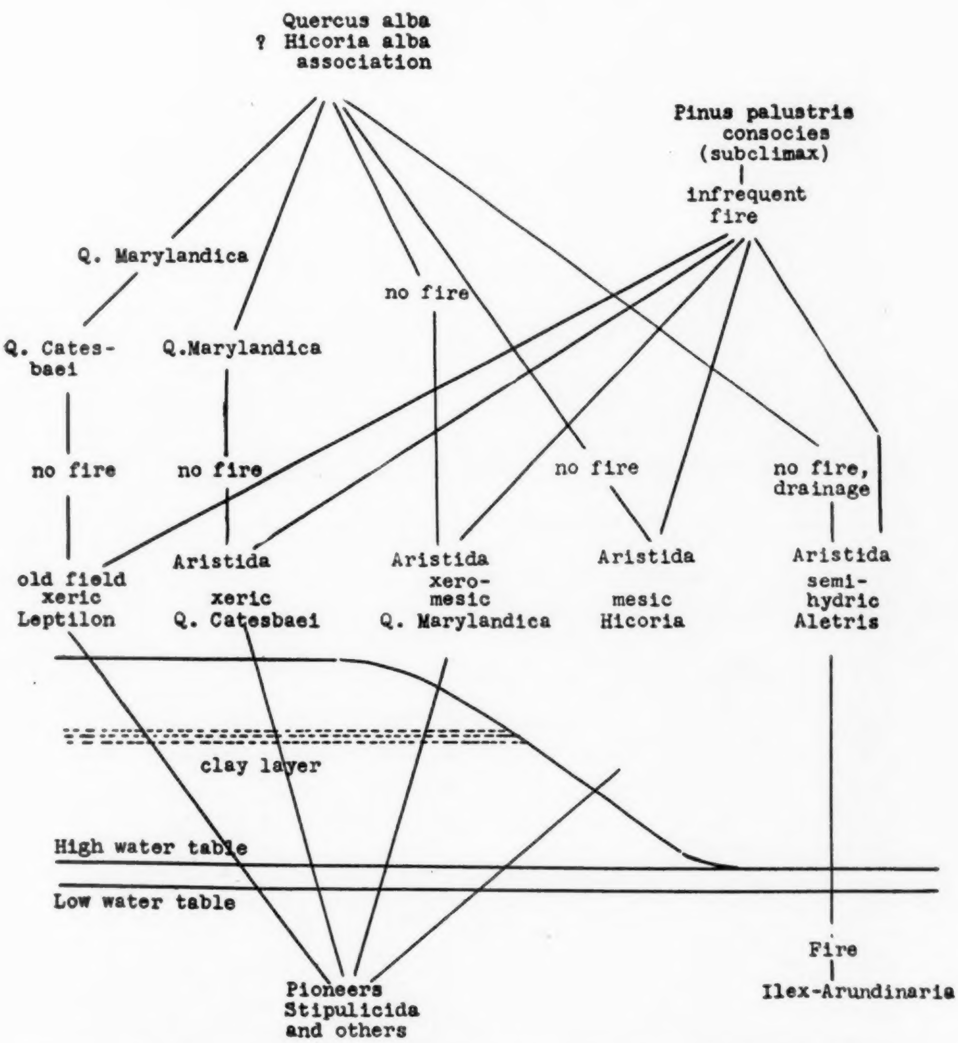

FIG. 21. Outline of seral movements on various medium to coarse sand habitats.

Distribution. Geographically the associes and its related medium to coarse sand habitat, are distributed in North Carolina chiefly in the southern half of the coastal plain. Only a few areas of any significance lie in the northern half. Outside of North Carolina there are practically no sites to the north in Virginia, wire grass being practically unknown in that state. To the south

are vast areas carrying the Quercus-Aristida associes. In Georgia and Alabama especially, are extensive acreages of unbroken fire-cursed areas of this type. The xeric associes is common in the northern half of Florida. In

FIG. 22. Winter view of turkey oak pioneer consocies near White Lake

FIG. 23. Summer view of xeric phase of the Aristida consocies near Station 1 of the Spout Springs transect.

Mississippi and Louisiana, the areas covered by this community are not so extensive while in eastern Texas some 6,000 square miles are reported.

Topography. The topography of these loose sand areas is typically hilly, almost invariably occurring either as low ridges or even high (100-200 ft.) hills. The "Sandhills" of Moore, Cumberland, Hoke, and Harnett counties are notable examples of the latter. The areas carrying what has been previously described as the hydric or semi-bog Aristida consocies exhibit the lowest relief a few feet only, yet these are always slightly undulatory. If very broad in a generally flat country of high water table, the average hydroperiod or period of flooding may be so great as to introduce the grass-sedge bog (Campulosus-Panicum Associes). It is thus correct to speak commonly of the North Carolina habitats as "sandhill" or "sand ridge," keeping in mind always that the texture of the sand must be of the coarser sort. The more rolling areas with much relief are of course to be found in the upper terraces, while the low sharp ridges, together with the broad poorly drained areas, are in the lower terraces close to the sea.

CLIMATIC FACTORS

The climatic factors play a secondary rôle. As will be shown in our evaporation studies, they may locally and temporarily exaggerate the natural dryness of the soil.

RELATIVE EVAPORATION

Anyone who tramps over the wire grass areas in summer where as little as a third of the surface carried the characteristic thin patches with their layer of white sand, will be impressed by the greater heat factor produced by reradiation. To what degree if any this reflection factor would affect the atmospheric temperature locally with concomitant increase in evaporation, was thought worthy of investigation. A narrow sand ridge (80 feet wide) near White Lake covered with white sand over which were scattered but a few pioneer plants, was chosen for the atmometer tests. On each side was shrub bog, the shrubs being about four feet high. Livingston standardized atmometers attached to graduated tubes for daily use were used, the exposure time extending from 9:00 a.m. to 3:00 p.m., the period of most intense radiation. The following are characteristic results:

	cc.
1. Middle of white sand ridge 6 in. above surface	25.1
2. Same as above, 5 ft. 7 in. above surface	24.6
3. Shrub bog, 60 ft. from ridge margin, 5 ft. 8 in. from ground or 20 in. above top of shrubs	19.2
4. Same as preceding, 4 ft. or at level of shrub tops	17.7
5. Same. 6 in. from ground, amid base of shrubs	16.5
6. Over nearby lake, 200 feet from middle of ridge, 40 feet from shore	15.5

All other measurements were consistent with these results, which definitely show on days of little wind and high radiation measurable differences in the relative humidity of locally contiguous areas.

In sandy soils with low water supplying power in the surface layer during drouth periods, high evaporation for juvenile shallow-rooted plants might locally prove critical. A few local contrasting conditions were tested with atmometers during single days. All measurements were made in midsummer on clear days. The Raleigh measurements were made on small specially prepared areas.

	Carolina Beach 7/6	White Lake 7/20	Raleigh 9/6	Raleigh 9/7
White sand surface	27.3	18.3	13.6	16.4
Dark sand	...	...	15.9	20.9
Leaf litter	29.1	20.7		
Tree shade	19.7	6.6		
Elevation of 40 cm. above sand	26.5	...		
Elevation of 12 cm.	...	13.8		

From these data it is apparent that evaporation is uniformly greater immediately over dark soil surfaces. This fact is to be correlated with the higher temperatures always found on these surfaces. It thus appears that heating of the air through reradiation when contrasted with that by conduction from the heat absorbing dark soil, is definitely less. These effects, it should be noted, are of significant intensity only near the soil surface, yet it is just here that in the germination and juvenile stages of plant establishment, they may well prove of life or death value. Both the white and dark soil surfaces which prevail in sandhill regions may be regarded as setting up local temperature conditions conducive to higher evaporating power of the air in contrast to those temperatures relating to vegetation or soils of medium value in light absorption.

Atmometry studies on the Spout Spring transect disclosed no differences great enough so that evaporation could be interpreted as a significant controlling factor in the local distribution of the plants on the area. While in certain areas local and temporary intensities of the climatic evaporation factor are not very great they may well prove very important in upsetting the water balance of superficially rooted plants and thus in the drouth periods add significantly to the xeric character of the coarse sand habitats. Many plants such as *Quercus Catesbaei* and *Baptisia villosa* (Fig. 24), unquestionably have their transpiration reduced by vertical leaf orientation. There are no Weather Bureau records of relative humidity from the Sandhill District. Our data indicate that were such data obtained, the relative humidity would average lower than in the surrounding regions.

TEMPERATURE

A thermograph was not at hand to follow the temperatures obtaining through the water testing periods at Spout Springs. Since the winds of the area under discussion are moderate, and especially so near the ground level, the water losses must be chiefly correlated with temperature. However, some

comparative temperature features related to surface and subsurface conditions are of more than passing interest (Table 1). All were taken on clear days sometime between 12:00 m. and 3:00 p.m. so as to gain comparative information concerning maxima. Many other temperature data were taken which are in entire agreement with those given. All temperatures are given in centigrade.

FIG. 24. Vertical orientation of leaves of *Baptisia villosa*.

The sharpest temperature gradient found was that between the upper and under side of a mass of leaf litter. Due to its dark color and consequent high absorption of radiation such extreme temperatures as 50°-60° C. may be commonly recorded. Such high temperatures, however, have little or no effect on the soil moisture condition, as is shown in the soil point data.

The rôle of the white sand cover where this is extensively developed is a very important one. By reflection of the radiant energy the subsurface temperatures are kept much lower, with concomitant conservation of available water. The heat, however, reradiated tends to heat up the air over white sandy areas. On still days this may produce a measurable difference in the evaporating power of the air (see p. 493). However, this effect is of minor importance with regard to the water balance in the plant, the more significant effect of the white sand cover being that of the soil water relation. This favorable condition, it must be remarked, is partially nullified by the well known fact that on a heat conduction basis the sandy soils warm up more rapidly than loam and clay.

Compared to more northerly sandy areas it is to be recognized that the more frequent higher temperatures of southern latitudes are from a soil standpoint alone distinctly conducive to more marked xerism.

Edaphic Factors

Geological Aspect. The geological factors in their primary control of the soil habitat are of preëminent importance. However, only a very brief discussion of them need be introduced here since they are remote factors which affect vegetation only indirectly. Of primary significance are those past conditions which, when the Lafayette and Columbian terraces were built, brought about the deposition of the coarser sands. For only on these soils are found the xeric consocies of the Quercus-Aristida associes dealt with in this study. Unquestionably the majority of the sand-hill deposits represent the work of water along sea shores, estuaries, and river beds. Aerial deposition has to a limited degree also occurred. On the younger and lower terraces, particularly near the positions of their escarpments, ridges of coarse sand may be observed which represent former offshore bars. Many of these are continuous for a mile or more, as are those of the Chowan Terrace south of Wilmington.

TABLE I. Temperatures; all taken between 12:00 m. and 3:00 p.m.

	Air Temp.	Surf. White sand	Surf. leaf litter	.5 cm. deep	3. cm.	5 cm.	10 cm.	14 cm.	36 cm.	Bog soil
White Lake 5/14/26	28°	38°			27°					16°
7/19/27	31°	38°	61°							
7/20/27 2.00 P.M.	33°	43°	57°	46°	39°	37°	34°	32°	26°	30°
	Beneat	h litter	32°		Shaded		Shaded			
	"	"	5cm.29°		26°		25.5			
Spout Spr. 4/7/29		46°	56°							
	Beneat	h litter	25°							
	Beneat	h white								
	sa	nd	26°							
5/23/29	30°	39°								
White Lake 8/24/26		44°		42°						
	1 cm. above surface			42°						
Air	5 cm. above surface			39°						
Air	10 cm. above surface			37°						

Not only is the texture of the sand important as a result of physiographic factors, but in many situations the nature of the underlying strata on which the sand mantle lies unconformably plays a prominent rôle. This fact is to be noted in the region known as the "Sandhills" in the south-central to east-central part of the state. Here the Lafayette sands lie on the Lower Cretaceous

Patuxent Formation, a stratum averaging 200 ft. or more in thickness and which was badly eroded before the late Pliocene sands were laid over them by the last invasion of the sea making contact with old Carolina gneiss of the present Piedmont Region. The Patuxent layer is composed of alternating layers of clay and arkosic sands, the clay layers being of particular importance because of their plastic water-holding and water-impervious nature. All through the "Sandhills" these clay layers play a very important rôle in keeping the water table much higher than it otherwise would be. In numerous places like the site of our Spout Springs transect (Fig. 18) a plastic layer located well above the valley base causes perennial seepage along the lower slopes and results in what may be called "slope bogs" of both the shrub and grass-sedge types. These slope bogs are unique and are found in North Carolina only in the Sandhill Region where the geological conditions are such as to make them possible. For our study these elevated water tables developed on the Patuxent clays are most significant, for they introduce a soil water level of unusual stability. The fluctuation, under the rainfall distribution of the region, is not wide (1-3 ft.) and responses are very slow. Plant zonation under these conditions is very definite.

An effect of wind transportation is noted in many localities and is particularly prominent in the Sandhills. We refer to the surface layer (0-1 ft.) having a notably finer texture than that of the deeper sand. This finer texture is due to the windblown material from the surrounding region. Dust storms may be observed at the present time.

Another primary control of geological character is that of the resultant topography of coarse sandy areas. In contrast to the much eroded undulating terrain of the sandhill country, there are on the lower three terraces (the Wicomico, Chowan, and to a very limited extent on the Pamlico) extensive upland areas essentially flat in character which are underlaid at a shallow depth with a non-draining layer. These develop a high water table under frequent and heavy rains and create temporarily a bog-like, flooded upland. Such areas are very distinctive, as has already been pointed out in the discussion of the semi-bog phase of the Aristida consocies.

Profile. Only a typical profile like that at Station 1, Spout Springs transect need be given. The first very thin (1/4 in.) layer of coarse white sand occurs between the tussocks of wire grass and is formed through the sorting action of moving surface water during heavy rains, when water accumulates temporarily on the surface.

Humus bearing layer. In the profile at Station 1 (Fig. 25) it is apparent that a thin black humus bearing layer is present just beneath the very thin (1/4 in.) mantle of white sand. This humus layer presents some problems of more than passing interest. It is not at all uniform, being found thicker and more concentrated in the small local bare areas covered by the white sand than in the places not so covered and in the soil beneath the tussocks. This

humus is, of course, chiefly formed from the roots of wire grass. Under the white sand the soil water is retained longer through prevention of excessive soil heating, hence the root response. Supporting the theory of very slow decay is the fact that throughout the humus zone numerous partially disintegrated roots are found, so that the layer appears somewhat similar to a layer of fibrous peat.

WATER RELATIONS

As is universally recognized the water relations in the sandy soils are of primary importance. We shall here concisely present our quantitative data dealing with this factor, holding over the discussion of factor interrelations and factor correlations with the vegetation to the third and last section of this paper.

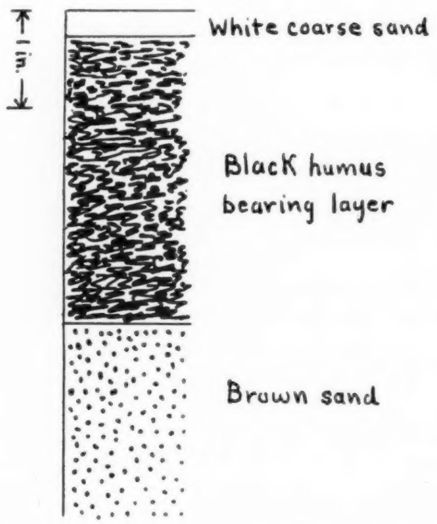

FIG. 25. Profile in local white sand area at Station 1, Spout Springs transect.

Water supplying power of the soil. For the measurement of this major factor Livingston soil points were used, following the method developed by Livingston (6), Wilson (14), and others. The exposure interval was one hour. Our fullest records were made on the transect near Spout Springs (Fig. 18) where, as shown in the discussion of the vegetation, striking zonation occurs under the varying conditions of water.

To show the water supplying power 12 hours after a heavy rain, tests were made at six stations on the transect on March 27, 1929. The rain was at night and the following day was cloudy and cool with a moderate wind, so relatively little water was lost by evaporation. The soil points were pressed into the surface of the ground, the center of the exposed area being 3 cm. beneath the surface. The readings are direct being in milligrams of water absorbed in 1 hour.

Station 1. *Q. Catesbaei*	2190
Station 2. Ecotone to *Q. Marylandica*	2035
Station 4. Middle of Hicoria	1515
Station 5. Ecotone Aristida-Panicum	1535
Station 5a. Ecotone Panicum-Arundinaria (Bog)	4160

It must be pointed out that the unexpected decrease in the mesic zones is due to the fact that the surface soil on the lower slope is composed of much coarser sand, due to washing effects in the heavy rains.

The next readings are those found at different depths in the deep sand of the hilltop at Station 1.

	March 27 12 hours after rain	April 3 4 days after rain
3 cm.	2065	1000
30 cm.	2000	1420
60 cm.	1640	1215
90 cm.	1050	800

The presence of coarser sand in the subsoil, with its low water holding capacity and low capillary function, explains the striking decrease at the 60 and 90 cm. depths. This correlation is very significant in relation to the very long drought periods.

Next will be given two series (April, May) showing the decrease in water supplying power at stations on the Spout Springs transect. The April readings began at 2:00 p.m., April 3. The last rain was on March 30, four days preceding. The weather was fair and all readings were at a depth of 3 cm.

	Apr. 3	Apr. 4	Apr. 7
Station 1. *Q. Catesbaei*			
Thin cover white sand	1000	1040	550
Leaf litter	1000	....	...
Station 2. Ecotone to *Q. Mary.*	370	540	280
Station 3. Middle *Q. Mary.*	810	1325	180
Station 4. Middle Hicoria	1255	235	250

From these 3 cm. depth records it became apparent that, due to wide variation in texture of the surface soil through washing effects, it would be desirable to obtain a series giving the decrease following rain at 30 cm. depth Such a series for 6 rainless days following a heavy precipitation was obtained between May 21 and 27. Readings at 3 cm. depths were also obtained at Stations 1, 4, and 5.

		May 23	24	25	27	28
Station 1.	3 cm.	475	130	130	10	130
	30 cm.	1105	900	835	620	905
Station 2a.	30 cm.	140	250	855	1355	
Station 2b.	30 cm.	2880	2925	2245	2890	2050
Station 3.	30 cm.	1310	930	1070	620	
Station 4.	3 cm.		205	5	0	50
	30 cm.	630	905	645	545	20
Station 5.	3 cm.	135	390	490	275	
	30 cm.	Water table.				

Of interest in the above series is the expected rapid decrease in water-supplying power at the 3 cm. depth. Under the May average clear day evaporation conditions the critical point for seedling plants with shallow roots would be between 100 and 200, hence it is apparent that but three days are needed to bring the water-supplying power to the danger point. The influence of the terrace-forming plastic layer in developing a temporary suspended water table is seen in the increase shown at Station 2a. The large amounts shown at 2b are due to the fact that the soil points were pressed into this plastic layer, which with its high capillary function gave high readings. The anomalous very low records at the surface in the mesic Hicoria zone have already been mentioned and explained but it is of interest to note that with the water table but 40 cm. below the 30 cm. level the readings are here remarkably low. The one datum (3395) at 60 cm. shows the influence of capillary forces in bringing ample water to the point.

The data taken September 3, four days after rain, agree very closely with those for May 25, which cover a late spring dry period. During both periods clear weather prevailed. The data from Station 5 which was but 30 cm. above the water table show that on clear drying days the surface layer dries out more rapidly than capillary action can wet it. On a cloudy cool day of high humidity (May 29) the surface layer at 27 cm. above the water table gave 2325. For a restricted zone here a wide fluctuation in water content occurs and this is controlled by changing humidity conditions. The lowest measurement recorded at the deeper levels in the *Q. Catesbaei* zone was made June 23, 1926 following a rainless period of over two months, the last general rain and the only one so far as could be learned falling on the area on April 12-13: 3 cm., 0; 30 cm., 0; 60 cm., 150; and 90 cm., 500. From these data it is seen that during an occasional extended drouth period the water-supplying power of deeper soil layers may fall to a critical point. The occasional mesic herb, shrub, or tree that has successfully run the gauntlet of the surface conditions in its juvenile stages will now be eliminated. Such plants as *Tithymalopsis ipecacuanhae* are successful in running this gauntlet, through the xeric adaptation of a rapidly growing and later thickened tap-root (Fig. 26).

At the coarse sand station near White Lake (see datum under texture, page 502) the following results were obtained. These are given for their comparative value since the time of the last rain was not known.

Cladonia	3 cm.	0
Cladonia	5 cm.	200
Cladonia	30 cm.	120
Aristida	3 cm.	1500
Ilex	3 cm.	800

At this station the permanent water table is but 3 ft. beneath the surface but the capillary function is so low that only the soil lying 6 inches over it is

affected. The difference between the Cladonia and Aristida while not large is probably very significant for Aristida is never a pioneer on the coarse sands. Measurements made at the 3 cm. depth under white sand and under leaf litter gave no significant differences. The mulching effect of the litter material apparently is equivalent to the heat reflection effect of the thin white sand layer, with its resultant prevention of high soil temperature and consequent water loss.

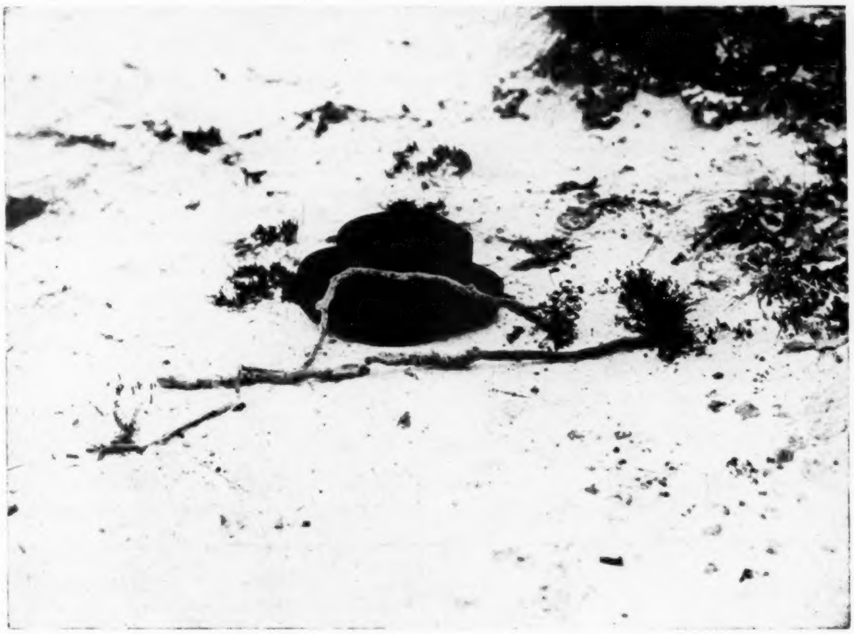

FIG. 26. *Tithymalopsis Ipecacuanhae.* Tap-root type. A pioneer.

A mile and a half from the Spout Springs transect is a hilltop covered by loblolly pine *(P. taeda)*, a tree never seen on deep medium to coarse sands. On July 24, 1929, 3 days after the last rain, measurements were made about the same time in both the *Q. Catesbaei* zone and at the loblolly pine hill.

O. Catesbaei (Norfolk sand)		*Pinus taeda* (Hoffman sandy loam)	
3 cm.	790	3 cm.	490
30 cm.	1165	30 cm.	2590

Cecil clay loam of a wooded ridge top at Raleigh was also tested on April 8, 1929. This may be contrasted with data taken on April 7 at Spout Springs, the last rain in both places having occurred on March 30.

Q. Catesbaei (Norfolk sand)		*Q. alba* (Cecil clay loam)	
3 cm.	550	3 cm.	215
30 cm.	835	30 cm.	1835

On the same sites during July the following were found:

Q. Catesbaei 3 days without rain		*Q. alba* 4 days without rain	Shaded	Unshaded
3 cm.	790	3 cm.	875	510
30 cm.	1165	30 cm.	2325	1930

From these data from contrasting soil types it may be readily seen that the 30 cm. depth is of far more significance than any shallower one. The full discussion of this matter will be reserved until later, when the field data may be correlated with those from pot phytometers.

Texture. The texture factor is of preëminent importance, for it not only exerts control of soil water conditions but in the matter of relative nutrient relations its rôle is a profound one. The following mechanical anlayses will

TABLE II. Soil Textures; Spout Springs Transect.

	Station 1			
	0–6 in.	6–12 in.	2 ft.	4 ft.
Fine gravel	2.90%	2.5 %	5.94%	9.35%
Coarse sand	17.15	18.17	25.71	26.15
Medium sand	32.33	72.64	37.89	37.82
Fine sand	35.04	.20	25.38	22.09
Very fine sand, etc.	12.03	5.68	4.58	4.02
	99.45	99.19	99.50	99.43

	Station 3		Station 4	
	0–6 in	6–12 in.	0–6 in.	6–12 in.
Fine gravel	8.92%	0.67%	7.56%	6.29%
Coarse sand	25.34	2.87	21.45	20.21
Medium sand	32.14	7.17	33.56	30.26
Fine sand	22.42	19.61	25.98	30.25
Very fine sand, etc.	10.81	68.93	10.52	11.92
	99.61	99.25	99.07	98.93

	Station 5		White Lake Ridge: Pioneer Stage	Pinus taeda ridge top near Spout Springs transect.
	0–6 in	6–12 in.	0–6 in.	0–6 in.
Coarse gravel	.....	.....	.....	4.16%
Fine gravel	10.43%	11.19%	5.72%	10.37
Coarse sand	39.27	41.50	69.28	26.66
Medium sand	33.33	30.29	24.33	18.85
Fine sand	12.43	11.45	.21	16.84
Very fine sand , etc.	4.05	4.73	.02	22.36
	99.51	99.16	99.56	99.24

bring out the range of texture in the *Aristida stricta* areas. The first series is that of the Spout Springs soils. The figures in Table II are given in percentages of the grades found.

The sand ridge at White Lake from which the very coarse sand was taken is shown in Fig. 27 at the right. The surface of this ridge is only 3 feet above the permanent water table.

Organic matter. Soil flora and water content. Tables III, IV, and V present information concerning the number of bacteria and actinomyces, actinomyces alone, and fungi, together with total carbon, total nitrogen, organic matter and water content of soil at four stations of the Spout Springs transect.

TABLE III. Organic matter, soil flora and water content based on collections made at Spout Springs, April 18, 1929. All figures on basis of oven dry soil.

		Moisture %	Bacteria & Act.	Act.	Fungi	Total C %	Total N %	Organic Matter %	Hygroscopic Water %
Q. Catesbaei...	0–6″	7.7	1,050,000	680,000	24,000	0.43	0.0137	0.75	0.25
Station 1	6–12″	5.6	2,176,000	300,000	3,200	0.15	0.0067	0.27	0.20
Q. Marylandica	0–6″	14.3	896,000	340,000	29,000	1.30	0.034	2.28	0.81
Station 2	6–12″	30.7	209,000	155,000	1,700	0.64	0.026	1.12	2.01
Hicoria.......	0–6″	7.4	1,160,000	640,000	36,000	1.0	0.025	1.75	0.35
Station 4	6–12″	5.5	697,000	697,000	40,000	0.32	0.009	0.56	0.15
Arundinaria–Aristida transition...	0–6″	24.5	1,883,000	647,000	76,000	2.33	0.072	4.08	0.86
Station 5	6–12″	26.4	556,000	60,000	10,000	0.95	0.0.6	1.66	0.55

TABLE IV. Microörganism data based on collections made at Spout Springs, September 21, 1929. All figures on basis of oven dry soil.

		Moisture %	B & A	Act.	Fungi
Q. Catesbaei..................	0-6″	8.9	1,024,000	601,000	38,000
Station 1	6-12″	5.1	535,000	370,000	3,900
Q. Marylandica...............	0-6″	13.1	1,174,000	552,000	18,000
Station 2	6-12″	27.4	280,000	193,000	900
Hicoria.......................	0-6″	7.3	674,000	386,000	25,000
Station 4	6-12″	6.3	553,000	306,000	10,600
Arundinaria..................	0-6″	10.4	1,175,000	663,000	12,500
Station 5	6-12″	22.7	314,000	117,000	3,300

Microflora. The total numbers of bacteria and actinomyces are considerably lower than those found in average mesic soils. Attention should be called to the fact that in the micro-population the actinomyces number is

relatively large in proportion to the number of bacteria. This may be due to the ability of the actinomyces to survive and multiply in a soil undergoing great changes in water content with the dry state predominating. The fungi are also comparatively low in number. The high number in the subsoil of the hickory zone represents an exceptional situation. A later count (Table IV) showed the number to be consistent with other stations.

FIG. 27. Ecotone or transition region between low sand ridge and shrub bog near White Lake. Turkey oaks at right with extensive bare areas. Pinus taeda and palustris at left.

TABLE V. Nitrogen data based on collections made at Spout Springs, September 13, 1929. All figures on basis of oven dry soil.

		Moisture	Nitrates	Ammonia N. Mg. per 100 gms Gms. dry soil
Q. Catesbaei	0-6″	5.4	None	1.5
Station 1	6-12″	4.1	None	0.83
Q. Marylandica	0-6″	7.5	None	0.86
Station 2	6-12″	16.4	None	trace
Hicoria	0-6″	6.4	None	0.43
Station 4	6-12″	5.9	None	0.43
Arundinaria	0-6″	14.8	None	1.63
Station 5	....	24.0	None	0.5

The data pertaining to total carbon and total nitrogen are particularly informing. At all stations, the total carbon and organic matter are very much

higher in the 1-6 in. layer than the layer below. As has been stated a humus-bearing layer located at or near the surface is sharply defined in the Aristida consocies areas, varying from 1-3 in. in thickness.

From Table V it is apparent that nitrogen content is very low. In accordance with expectation that of the humus zone is much higher than the non-humus bearing subsoil. Nitrates cannot be demonstrated. The demonstrable mobilized nitrogen occurs as ammonia as shown in Table V. Thrifty plants, like *Lupinus diffusus*, are commonly surrounded by a bare area (Fig. 28) which should probably be correlated with nutritional competition. Competition for water may be excluded, for there is no incoming of other plants in wet years.

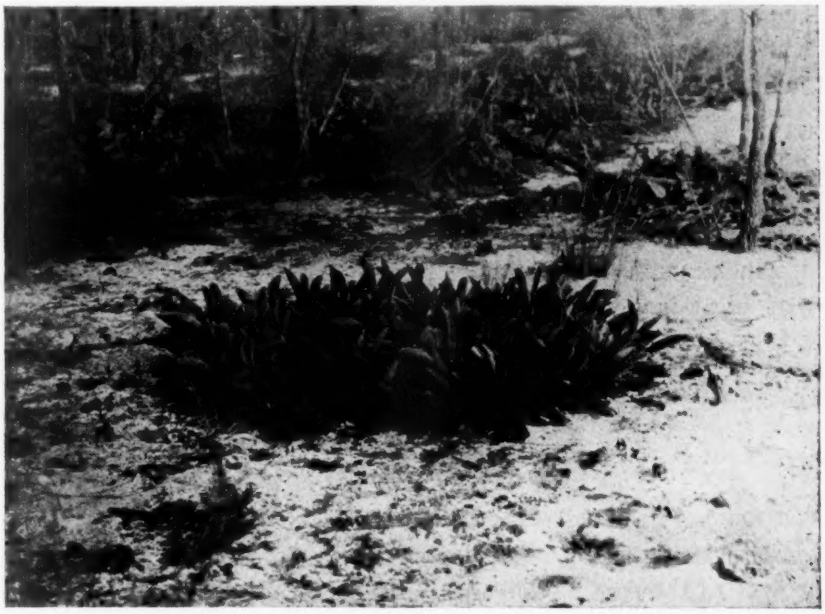

FIG. 28. *Lupinus diffusus*, a characteristic sandhill lupine. Note the bare area around the plant. This is indicative of nutritional competition.

Particularly significant is the extremely high C/N ratio. The usual ratio in agricultural soils is approximately 10:1. In the sandhill soils this ratio varies from 25:1 to 40:1. In this fact of the very high C/N ratio a further explanation of the low bacterial content and activity is found.

CO_2 evolution. Since the evolution of CO_2 from a soil is a valuable index to the activity of the microflora and indirectly to the soil fertility, a comparison was made of the sandhill soil and a manured garden soil in this respect. The results are shown in the Table VI. The CO_2 evolution of the sandhill soil was very low under all the moisture conditions, being, of course, the lowest in the air dry soil. Under optimum conditions of water (60% of saturation capacity) the sandhill soil gave off approximately 20% as much

CO_2 as the garden soil under similar moisture conditions. These results are in accord with those which might be expected from the bacterial counts and the high C/N ratio.

TABLE VI. Evolution of CO_2 from sandhill soil and garden soil. Figures indicate milligrams of C as CO_2 per 100 drams of dry soil.

	Moisture	1-7 da.	7-14 da.	14-21 da.	Total
1. Garden Soil	7.3%	4.3	2.7	3.3	10.3
2. Garden Soil	7.3	5.6	4.5	3.9	14.0
3. Garden Soil	32.2% (Opt.)	46.9	26.4	17.9	101.2
4. Garden Soil	32.2% (Opt.)	46.7	27.0	7.1	80.8
5. S. Hill	22.8% (Opt.)	9.7	5.8	5.4	20.9
6. S. Hill	22.8% (Opt.)	10.3	6.6	5.8	22.7
7. S. Hill	16%	4.1	3.8	4.1	12.0
8. S. Hill	16%	7.2	4.1	3.0	14.3
9. S. Hill	10%	8.7	5.2	4.4	18.3
10. S. Hill	10%	6.4	4.3	3.8	14.5
11. S. Hill	1.8% air dry	3.0	1.1	1.5	5.6
12. S. Hill	1.8% air dry	1.3	0.9	1.0	3.2

Hydrogen-ion concentration. The soils under consideration in this paper are uniformly mediacid, the range being between pH 4.5 and 5.0. A few records of many made will suffice:

Aristida consocies. Rowes Bridge	
xeric phase	4.8
hydric phase	4.8
Q. Castebaei. Spout Springs	5.0
Aristida consocies. White Lake	4.5

A test made of the soil (Hoffman sandy loam) carrying the *Pinus taeda* consocies on a neighboring hill at Spout Springs (see data under "water supplying power of the soil") gave a pH of 5.6. It appears that as one goes into the finer and more mesic soils in the coastal plain region the acidity becomes less. The H-ion factor is, however, merely a concomitant of other factors and does not in these soils exert a direct control so far as known.

PHYTOMETER STUDIES

First Experiment. Soil (Norfolk sand) was brought from the Spout Springs transect area (Station 1) and the following variants in soil treatment were set up in the greenhouse, each test being run in duplicate. The mesic tomato was used and proved to be a very desirable plant in bringing out the relation between low nutrient and the water factor.

In getting the soil, the pots were taken to Spout Springs and filled, care being taken to place the surface dark layer of fibrous, root-filled soil on top of the loose sand beneath. The treatment of the pots is given in Table VII.

TABLE VII. Pot tests with Norfolk sand to show significance of nutrient and water factors.

1. 1 watering No nutrients	2. 1 watering nutrient sol. 1 gm. $NaNO_3$ in 250 cc.	3. 1 watering manure	4. 1 watering No nutrients Leaf mulch
5. 1 watering No nutrients Sand mulch	6. Continued watering. Nutrient Solution. 1 gm. $NaNO_3$ in 250 cc.	7. Continued watering. No nutrients	8. Continued watering. 60 gm. Manure
9. 1 watering All humus	10. Continued watering All humus	11. Washed sand No nutrients Continued watering	12. 1 watering No nutrients No cover

A similar set of pots containing Cecil clay was started at the same time, since it was thought desirable to test a soil of very different texture. 1a, 2a, etc., are the same except Cecil clay loam was used as soil medium. The results are summarized in Table VIII.

TABLE VIII. Results of phytometer test (Table 6). Data in terms of cotyledon length in mm. Figures in parentheses refer to length of secondary leaves if these had appeared.

	9 days	18 days	27 days	39 days
1	8	9	wilted	dead
1a	12	14	15 (5)	wilted
2	13	19	19 (5)	dead
2a	16	23	23 (10)	wilted
3	11	17	17 (8)	dead
3a	12	14	15 (3)	wilted
4	9	9	wilting	dead
4a	10	13	11 (3)	dead
5	9	14	14 (8)	15 (1 pot)
5a	9	16	12 (3)	dead
6	14	23	23 (15)	16 (25)
6a	16	14	25 (20)	20 (35)
7	9	14	14 (3)	14 (9)
7a	12	10	15 (5)	15 (15)
8	11	13 (2)	13 (6)	13 (13)
8a	8	16 (2)	17 (5)	18 (15)
9	8	11 (1)	11 (2)	11 (4)
10	9	11	11 (3)	11 (3)
11	8	11	11 (4)	11 (10)
12	9	wilting	dead	dead
12a	12	12	wilted	dead

In the Table IX the data on the water condition of the pots are given.

For pots 3 and 5, giving echards respectively of 3.3 and 3.9, the water-supplying power indices were 40 and 150. In this connection it is interesting to note that Livingston and Koketsu (6) found the water supplying power

TABLE IX. Echard (percentage of water at wilting point) in pots.

	Pot. No.	Days before wilting	Echard 7.		
			Top	Middle	Bottom
Sand................	1	18	1.18		
	2	27	1.14	3.24	3.96
	21	29	1.15	3.33	4.12
Clay................	2a	29	5.33	12.43	13.25
	12a	27	5.06	11.06	11.70

at the echard for coleus and wheat was approximately 100 for a two hour exposure period of the soil points in sand. The average they found regardless of soil texture was 85.

Soil temperature. The difference between the pots with dark soil (humus layer) exposed at the surface and those with a thin white sand mulch during the midday period proved to be very marked, as the following observations at noon on April 15 show

Pots No. 2	3	4	5	3a	5a
Temp. 48°	42°	52.5°	36.°	39.5°	32.7°C.

The data show some very definite contrasts. It will be best, however, to defer the interpretation of these results until later, when they may be discussed along with the information gained in the following two experiments.

Second Experiment. The results of this test may be best shown in a diagram (Fig. 29), all plants being drawn to the same scale. The different treatments are given under each average plant. The experiment ran for 22 days beginning May 14. By "no water" we mean that no water was added after the original soaking of the soil to initiate germination. By "brown sand," we refer to subsoil sand taken from the four foot level. Fig. 29 shows that watered garden soil was very much more favorable for growth than the full nutrient or the manured soil. In the nutrient element test nitrogen was slightly more important than either potassium or phosphorus. Those plants with a better vegetative structure because of early shading or of nutrients present outlived the weaker, untreated ones, which fact confirmed the results of the first experiment.

Third Experiment. Tolerance of *Aristida stricta* and *Andropogon Virginicus* to flooding or long hydroperiod were tested. Pots of wire grass and broom sedge *(Andropogon Virginicus)* in their own native soil were placed in large jars filled with water to within a half inch of the soil surface. The test started on April 4. After 100 days, both grasses were in good condition, except that the broom sedge showed a tendency to redden the leaves. It was then thought desirable to transplant wire grass from sand to black bog soil. In sixteen days it was dead while the control transplanted with sand

remained alive and normal. The broom sedge in bog soil remained alive and grew normally in both drained and flooded bog soils.

Interpretation of phytometer data. Perhaps the most important result was the demonstration of the relation of nutrients to survival in the face of a decreasing water supply. Uniformly, early death was the result where the nutrient content was so low as to inhibit root growth of seedlings so that the roots could not keep ahead of the descending echard zone. This zone goes downward at a rapid rate in the surface layer of sandy soil fol-

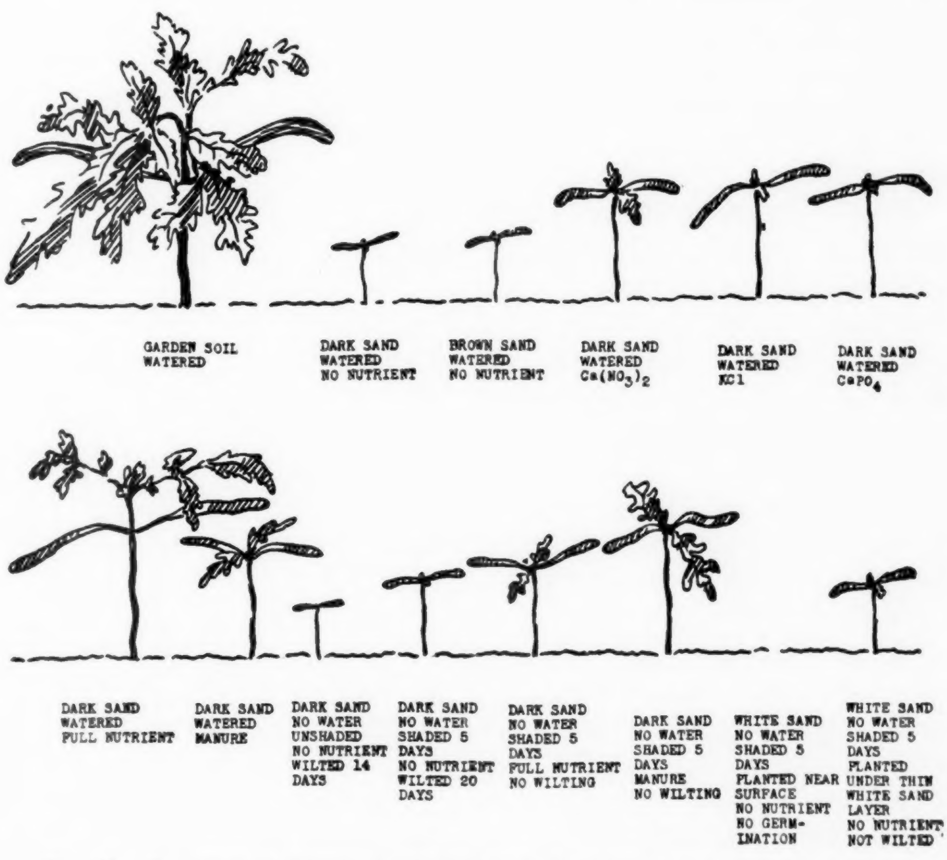

FIG. 29. Response of tomato plants under various conditions of tests in pots.

lowing rain and in the low nutrient factor which is emphasized in nature by the competition of resident plants, the seedling mesic plant is unable to develop roots with sufficient rapidity to maintain its proper water balance. In medium to coarse sandy soils the roots must grow to the water which is carried as films on the soil particles, since under low water conditions this water moves very slowly if at all by capillarity. This point will be again taken up in the correlation of the phytometer data with those from the field. Differential survival was often observed in the same fertilized pot where the smaller plants with shallow and more limited root system uniformly died

out first. The number of plants was too restricted to introduce competition as a serious factor in these instances.

The length of survival on clay was not as great as would be thought from its much greater water holding capacity. Examination of our pots disclosed the fact that the native red clay used was of lumpy structure and the roots were confined chiefly to the sides of crevices, a situation seldom present in nature. The clay plants under decreasing water supply uniformly showed slow wilting, many days being involved in bringing the plant to its death, while on the other hand the plants in sand died out quickly, one warm day after wilting began, commonly being sufficient to eliminate them.

In conducting these pot experiments it was early recognized that to get a stand on the sandy soil, cheese cloth protection would be necessary for a few days. In those pots not protected, early and rapid elimination took place.

In accordance with expectations the watered pots to which nutrients had been added, synthetic nutrients in the second experiment did not bring the response that cow manure did. But both of these were far ahead of the insignificant plants produced on untreated soil. Nitrate alone was better than manure, as shown in the first test. No difference could be noted between soil at the surface and the coarse soil taken from the 4 ft. level. With regard to the most needed nutrient elements a glance at the figures shows nitrogen to be most important, with K and P about alike. The latter element it should be mentioned when deficient prevents rapid root elongation (11), a function which is so necessary to survival if the water demand of the plant is moderate to large. The response to nutrients in the clay soil was essentially similar to that of sandy soils.

Of especial interest were the results obtained in our sand mulch experiments. Due to having a 12°C. hotter surface temperature the dark soil quickly dried to the echard before root growth under low nutrient content reached the deeper layers. The seedlings were then early eliminated. In the dark soil with the thin white sand cover so great was the reflection of heat rays as to result in the contrast above mentioned. In these pots the water content of the soil near the surface remained sufficiently high for the plants to become deeply rooted, though no growth beyond very small secondary leaves was possible on account of low nutrients. Seeds planted on or near the surface of this white sand layer gave no stand whatever. A thin mulch of leaf material showed no protective function. The high radiation absorption capacity of leaf material accounted for a similar heating up of the soil as was observed in the dark soil pots. The influence of humus in the sandy soils is shown in the case of the pots filled throughout with the humus-bearing soil. The plants long survived the controls with non-humus subsoil, but under the low nutrient condition made little growth. The wa-

tered pots did no better, again showing the importance of the low nutrient factor.

A number of soil point readings taken in the bottom layer of pots (nutrient or sand mulch) in which the plants had survived and had grown roots throughout the soil, gave critical indices around 100. This was under greenhouse conditions of relatively high humidity. Under late spring and summer summer conditions in the open this index at wilting would be much higher.

Field test. The results of a field test carried out with plantings of corn, sunflower, and soybeans were in accordance with our pot studies. The unmanured plots died out sooner than the manured ones, the plants on the latter showing twice the size of the former. The growing season had no extended drought periods, yet the differential of nutrient content and its effect on root growth, making possible more satisfactory water absorption, was very marked.

General Discussion

In facing the problems presented by the vegetation of the coarser sandy soils under Southern climatic conditions, we believe the relation of the nutrient and water factors as these are related to root growth is of paramount importance. The hypothesis is presented here that the low capillary function of the sandy soils necessitates continual root growth to reach newer supplies of water in drought periods. Hence the presence of nutrients is very important in the case of mesic species if these are to carry on sufficient root elongation to gain enough water for maintaining their relatively high transpiration. Since the native loose, deep sands are notoriously low in nutrients, this therefore constitutes a factor, which, supplementing other factors, is critical for the establishment of mesic vegetation. To state the situation conversely it may be said that under a low nutrient condition which inhibits growth, only those plants can survive which restrict water outgo, since in the sand, the roots with inhibited growth may reach only a limited amount of water during droughts.

This combination of factors tending toward xerism is most critical for the germination and juvenile stages of the plant's development. In these stages the usual inter-rain periods of spring and summer introduce critical drought conditions for the shallow roots and only the xeric forms survive. This accounts in part for the absence of any notable immigration of mesic types in average or even in wet years. Basing our conception of the critical soil water conditions upon the soil point index of 100 we note that in May it takes the surface layer (3 cm. depth) only 3 days to reach the danger region. This fact coupled with the demonstration in our pot studies shows conclusively what a difficult gauntlet the germinating plant runs between low nutrient and low capillarity. So severe is this surface soil condition between rains, it is believed that even the native xeric inhabitant

of the sandhills may become established only during the wetter years of closely spaced rains.

With the soil point index of the echard lying near 100 it is clear that satisfactory conditions for normal growth of the xeric plants must be even higher. It is thus interesting to call attention here to the data from our soil point records which indicate that the deeper layers (4 or more feet in the deep sand of the Spout Springs type) remain for long periods between rains at about 500. This figure is probably very close to the necessary water-supplying power to carry the native xeric vegetation under low nutrient, while the more mesic plants such as the black jack oak demand a higher index, which may be had only in the clay or iron cemented sand layers.

It is of significance in this connection to note that in soil point studies made on blue-grass cover in Baltimore (Wilson, 14) 600 was the critical index where the plants began to suffer with the wilting point at 100. These plants were in loam soil where the available water for a restricted root system through the function of high capillarity would be much greater than in the coarse sand with low capillarity. Here the roots must grow for the water so to speak and under low nutrient the inhibited growth makes the selection of xeric leaved forms inevitable with the consequent isolation of the distinctive xeric phase community. A corollary effect intensifying the foregoing situation in Aristida areas which has not yet been mentioned is the factor of competition for both nutrients and water which is presented to newly introduced plants by the vegetation already present. Preëminent here is the wire grass with most of its roots within the first 4 inches of soil.

The number and extent of the bare areas is to be related to this nutrient competition factor as this has its effect already on the water relation through inhibition of root growth. There can be little doubt that the wire grass, the only real dominant and cover plant in the sandhill regions under fire, is playing a most important rôle as competitor and this is far more significant as regards nutrient than water. This conception may be confirmed anywhere in the sandhills where the weed vegetation (horseweed) has come into old fields bordering native wire grass with bare areas between the tussocks. In seasons of frequent rains with ample opportunity for the weeds to appear in the bare areas, none appear while thousands come up a few feet away on the abandoned field.

In connection with the sterility problem, attention may well be again directed to the concomitant factors of low bacterial count, low CO_2 evolution, low total N, and extremely high C/N ratio. All of these factors operating in the surface soil (0-1 ft.) are most important in the cause and effect cycle tending toward infertile conditions. The relation of low fertility to succession is important. Even without fire, the fertility of these course sand soils will improve very slowly. But since the mesic vegetation in the deep sands is dependent upon nutrient, this factor is raised to a limiting one, with the

result that the hickory consociation would not appear for an unusually long period, if at all.

As another corollary to the main thesis, attention should again be directed to the fact that these sandhill habitats are slightly drier climatically during clear midday periods, on account of the reflection of the sun's radiation into the atmosphere by the white sand areas. This phenomenon would be more pronounced over extensive areas as in the "Sandhills" of North Carolina while further eastward these soil localities are of restricted size and are surrounded by regions of medium radiation absorption such as pocosins, woodlands, or gray to dark sandy fields. This factor, present as it always is at the time of decreasing water supply, unquestionably hastens the critical period of upset of the water balance.

Though the surface layer of the sandhill soil because of storms contains more fine sand than the deeper layers (see reports of mechanical analysis), it is, however, not sufficiently great in amount to overcome the xeric effects described. And of these effects that resulting from competition for nutrients in this same layer is one of the most important. The coarse nature of the subsoil in the deep sand of typical sandhill country in the light of our conception may readily explain the distribution of the vegetation—particularly the woody plants. Every countryman in such regions knows that black jack oak when found on the tops and upper slopes of hills indicates a clay subsoil.

Under the prevailing condition of fire-removed leaf mold if a xero-mesic plant should successfully get established in a wet year, unless it can make contact with a substratum of higher water holding capacity and greater water supplying power than the coarse sand affords, the first extended drought will eliminate it. Of the trees only the long leaf pine and the turkey oak are sufficiently xeric to maintain themselves on a basis of nutrient-inhibited root growth through the occasional long drought period of two to three or more months.

As has already been noted in connection with the organization of the "phases" of the Aristida consocies on the sandhill slopes, the herbaceous dominance of wire-grass extends not only through the xero-mesic and mesic zones of black jack oak and hickory, but goes on to the permanent water table where the Aristida semi-bog phase occurs. These three latter conditions will now be dealt with.

Upon referring to the data on texture it is observed that the surface soil (1-6 in.) in both the slope areas of black jack and hickory of our transect is coarser than the soil on top of the hill. This fact is due to the washing effect of heavy rains, which in moving the surface sands downward carry the finer particles on to the base and leave the coarser ones on the slopes. In the presence of the washed coarse sand on the slopes there is an intensification of the xeric complex of conditions which is sufficiently great to largely prevent mesic herbaceous vegetation from profiting by the nearby clay layer with

higher water holding capacity or even one supporting above it a perennial water table. The woody plants with their germules arising from large seeds furnishing the primary root both water and nutrients (the latter being especially important) are able to make contact with the perennial water sources below and survive. Numerous xero-mesic herbaceous perennials (see lists) like the woody plants are also able to enter but they do not attain dominance. This phenomenon then brings about a telescoping of the xeric and xero-mesic herbaceous vegetation with the xero-mesic and mesic woody plants. Fire, it should be recognized, tends to accentuate this condition by holding the mesic wooded areas to an open stand and so resulting in ample light for the xeric herbaceous plants which are intolerant of deep shade. However, it has been repeatedly noted that in open stands of both turkey and black jack oaks the wire grass may be found growing under the trees, readily tolerating the shade of single trees.

To emphasize the great contrast between such a vegetation as the xeric phase of Aristida on deep, loose sand and one in a more mesic locality attention may be directed to the sharp local changes that may be observed in the sandhill country. Just a mile and a half from the position of our Spout Springs transect was a hill-top capped by red Patuxent iron-consolidated sand, which, as our soil point records showed, gave about twice the water supplying power of the sands. On this hilltop were the mesic oaks, white hickory, and dogwood and in the long-abandoned fields were good stands of 40 feet high *Pinus taeda* with *Danthonia sericea* as an herbaceous dominant. No wire grass was present. About the only plant common to the two areas was *Chrysopsis graminifolia*, found in the pine community.

In favorable years in the mesic zone a few mesic plants like the broom sedges get established but they never approach even subdominance. Apparently the extended droughts keep them down. Shallowly rooted for the most part and unable to use the water holding layers as the trees do, the critical low point for them is reached and they disappear. One bit of evidence for this interpretation is the limited size of the Andropogon tussocks.

Before leaving the problem of the influence of the coarser sand, mention should be made of the very instructive station at White Lake. Here the average water table was but 3 feet below the surface yet this soil, having 70 per cent coarse sand existed chiefly as bare area with only the widely scattered pioneer plants on it. It was, however, especially interesting to note the presence of a few relict plants of yellow jasmine (Gelsemium) and scuppernong grape (*Vitis rotundifolia*, Fig. 30) which had survived from an earlier period when forest cover prevailed.

The problem of the Aristida semi-bog remains. As already noted in the earlier portion on the vegetation this phase is distinguished by the fact that in medium to coarse sand areas of a semi-bog type, i.e., having alternating periods of low and high and high water table, the Aristida stricta is the only

highland sandhill herb which enters the area where in spite of the fact that it must share the habitat with a large array of Panicum consocies (Wells and Shunk, 12) or semi-bog species, it attains dominance. And if the soil habitat is not too wet, the dominance may locally be pure, so luxuriant a growth is made. Only the long leaf pine among the woody plants of the upland accompanies the wire grass in this semi-hydric habitat.

FIG. 30. Relict *Vitis rotundifolia* on low coarse sand ridge near White Lake.

There can be little question that this peculiar telescoping of vegetation in one community is related to the larger fluctuations of the water table introduced by the extended drought periods. This fluctuation on the dry side is intensified by the presence of an organic ortstein layer of shallow depth (25-40 cm.). Thus we have in our Aristida semi-bog areas a soil characterized by a most rapid and extreme swing in the water content. In periods of frequent rain the water table is persistently high; in the longer droughts the soil water content will drop to a very low point as far down as the ortstein, and since the plant roots do not penetrate this layer, only such xerophytes as those listed earlier may persist.

Level areas have been observed where the Aristida-ortstein complex was in sharp contact with shrub bog with no introduction whatever of slope. In such cases the ortstein disappeared and a soft deep humus filled subsoil was found beneath the shrubs. In the latter instance the swing of the water factor on the dry side would not be so great.

Extended surveys have not been made to determine the variation in depth of the ortstein layer. In the coarse sands, however, it would appear that a

much deeper non-draining layer would not account for a sufficiently high and stable water table to introduce semi-bog conditions.

The reason why Aristida does not also occur in the lower and wetter areas, which also lose their surface water during dry intervals, is probably because of the higher amount of organic matter accumulated in these areas. This entirely changes the nature of the soil. Not only is the water-holding capacity increased but the dissolved oxygen content is greatly reduced in contrast to that of sand with low organic content. Aristida transplanted to bog soil failed to survive.

The foregoing discussion has dealt only with the four phases of Aristida which are determined under frequent fire by the fundamental factors of texture and water table position. These four phases represent the initial stages of subseres which at present hardly make an advance before fire reduces them again. The sequence of the sere without fire has already been discussed. Attention here need again be directed to the fact that under the low initial nutrient content (especially nitrogen) seral progress would at first be extremely slow.

The general picture of the situation on the coarser sands is that of the operation of a number of interrelated factors all tending to exaggerate the xeric conditions. Chief among these are relatively high evaporating power of the air, excessive drainage, low capillarity, low nutrient operating with inhibited root growth, ready heating of soil because of low water content, low water content of plant structures predisposing these to fire, removal of leaf litter mulch by fire, and slow regeneration of vegetation following fire.

With regard to fire it may be emphasized that the number and severity of fires is greater in sandhill vegetation than in other vegetation because of the readiness with which sandhill plant materials will ignite. Fires may be started in wire grass on humid days when it would be impossible to initiate a fire in moister grass and shrubbery. The observation of fires going out when mesic vegetation is reached has also been observed repeatedly.

From all of the foregoing it is seen that a vicious circle is established between coarse sand, xeric vegetation, and fire. This accounts for the present major ecological features of the coastal plain.

Practical Aspects

Rôle of nutrients. Throughout the wide range of crops grown on the sandier soils the chief lesson given by our data is that of maintaining favorable nutrient content. During the growing season of 1930 a drought which lasted six weeks occurred in the sandhill peach district. Trees under good fertilization did not suffer, for root growth so necessary in reaching the restricted water supply carried as films on the sand particles, was sufficient. On the other hand trees in abandoned orchards or those that were diseased or weakened in any way were killed, since root growth was inhibited.

In choosing a site for an orchard the best would be that underlaid at a depth of 4 to 8 feet by clay. The black jack oak on uplands is the indicator of these sites. If the depth of overlying sand depth is less than 4 to 8 feet, prolonged drought will lower the water supply in the clay to the danger point. In the deeper sand with ample nutrients it would take an extraordinarily long drought to reduce the water to the true echard.

Blueberries. During the course of our studies an experiment with blueberries was carried on, since it was anticipated that the soils of the semi-hydric phase of wire grass would prove favorable. Some 20 plants of the recently developed giant blueberries were kindly furnished us by the Whitesbog Company, of New Jersey, and these were placed in a transect at Rowes Bridge in Pender County which extended from wet shrub bog up on the level semi-hydric wire grass semi-bog. No attention whatever was given these plants, neither cultivation nor nutrients. Those in the muck or wet part failed to do well. They made little growth and were severely attacked by insect pests. On the other hand plants in the moist wire grass area made an excellent growth and bore good sized clusters of fruit.

In the southeastern coastal counties there are thousands of acres of wire grass semi-bog lands which from our tests should prove excellent for blueberry culture. A possible danger might be from flooding in summer. Excess of water in the winter or dormant season would do no harm. If the site could be chosen so that partial drainage could be introduced this danger might readily be overcome. The addition of nutrients and protection from competition would be about the only cultural practices necessary. It is to be hoped a thorough trial of blueberries on such areas may be made by those farmers who have this type of land in their holdings.

Fire. The sandhill ground cover when occurring in thick enough stand to burn is the most inflammable vegetation in North Carolina. The most extreme care with burning material must always be exercised at any time of the year, from a day after a rain on until the next rain, or the wire grass will blaze and go up in smoke. Inhabitants of sandhill regions should not only practice the greatest individual caution but if real control is to be gained the male populace must be organized for fire fighting. In connection with fire control the following suggestion is offered and should be worthy of trial. Since wire grass does not soon return in broken ground and the weed flora that does come in is sparse, insignificant, and hardly capable of carrying fire, fire lanes of plowed land ought to prove valuable checks to ground fires on the tops and slopes of hills. Such lanes guarded by beaters should readily keep fire within bounds.

Forestry. Ecological data are of general interest to foresters. The one valuable tree of the coarser sands is the long leaf pine (*P. palustris,* Fig. 31). It will respond to the favorable water conditions and make a much better growth in the black jack oak areas than in the pure turkey oak. On or near

the terraces made by outcrops of clay layers, the trees are more numerous and grow rapidly (Fig. 32). The very thrifty tree is much more certain to survive fire than the stunted individuals on the deep sand. Hence in reforesta-

FIG. 31. Virgin long leaf pine on sand ridge in center of Angola Bay, a great peat bog.

FIG. 32. Long leaf pine regenerating successfully on terrace of a sandhill near the Spout Springs transect. Shrub bog in foreground, wire grass in distance.

tion the black jack oak and even the hickory zones should be used first, for on these results will be obtained most rapidly.

Indicators. In a period of expanding agriculture and of land sales for farm uses, no advice concerning acreage purchases can equal that given by the native vegetation. From such studies as those described in this paper it is very apparent that the areas carrying the extreme xeric Cladonia, the xeric Aristida, and the semi hydric Aristida are to be avoided for general agricultural purposes.

SUMMARY

1. Wire grass *(Aristida stricta)* is the universal indicator of the coarser sands excepting on pioneer sites (white, coarse sand bare areas). The range of the wire grass fire subclimax in relation to soil water is very great; viz., from the xeric upland sands through mesic subsoil conditions to the semi-hydric transition areas to bogs. Long leaf pine has the same range, and is in addition a pioneer on the coarsest sand bare areas. Both plants function as dominants in two associes, an unusual ecological phenomenon.

2. Full lists of the plants occurring in the pioneer stage, the xeric, wire grass consocies, the xero-mesic wire grass—black jack oak mictium the mesic wire grass—hickory mictium, and the semi-hydric or bog wire grass consocies, are given together with comments on the more significant species.

Outlines of the various seral movements are presented with suggestions as to the reaction and physiographic changes involved.

4. The habitat factors measured are: evaporating power of the air temperature, water supplying power of the soil, soil texture, organic matter, soil bacteria and actinomyces, total carbon, total nitrogen, nitrates, CO_2 evolution, H-ion concentration.

5. Pot phytometer studies were carried out under glass, which work disclosed the significance of the various major controlling factors.

6. Among the more important conclusions reached are the following: (a) The low capillarity of the sandy soils during drought periods necessitates continual root growth to reach newer supplies of water. Such growth is inhibited in a very low nutrient soil habitat, hence the impossibility of the occurrence of mesic species. Thus a relation is established between the nutrient content and available soil water which is of major importance. (b) Competition for nutrients at all times is of great significance. (c) An extremely high C/N ratio, low total N and very low CO_2 evolution all emphasize the extreme sterility of the native soil under the fire subclimax stages. (d) The xeric soil condition is supplemented by local emphasis of aerial aridity due to the reflection of radiation by the extensive white sand areas. (e) The xeric vegetation of the sandhills has a very low water content (extreme in wire grass), hence its readiness to burn. The destruction of the vegetation enhances the xeric character of the habitat. Thus a vicious circle is established in which the coarse sand, the xeric vegetation, and fire play the major rôles, the whole

resulting in the sandhill areas in remarkably stabilized fire subclimaxes of the four types previously mentioned.

7. Certain practical applications of this study may be pointed out: (a) Good fertilization must be carried out if crops are to successfully survive extended droughts. (b) The indicator plants mentioned would unquestionably help in accurately judging favorable sandhill sites. (c) Good growth of the highest grade blueberries was obtained on wire grass bog land of which there are thousands of acres now not in use. (d) Wire grass does not return for a long time after plowing, hence fire protection may be gained on restricted areas by plowing. (e) This paper presents much valuable habitat and vegetation information to guide foresters in the proper planting and later care of the long leaf pine forests which may be grown on all coarse sand sites.

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